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First inventory of the introduced and invasive mollusks in Mexico

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ABSTRACT

Early historical records are included in this first national inventory of species of mollusks introduced, whether intentionally or not, into Mexico by humans. Of the 56 exotic-invasive mollusks listed, 15 inhabit brackish and marine environments, 10 freshwater, and 31 are terrestrials. Thirty-six per cent of the introduced species come from Europe and the Mediterranean, 18% from Asia-Australia-New Zealand, 46 % are cryptogenic, coming from different regions of the planet, and the origin of several others is uncertain. The best-represented families are Mytilidae, Teredinidae (brackish and marine), Ampullariidae, Thiariidae, and Planorbidae (freshwater), and Helicidae, Agriolimacidae, Limacidae, Subulinidae, and Vallonidae (terrestrial). They involve *Mytilus galloprovincialis* Lamark, 1819, *Pomacea canaliculata*, Lamark, 1819, and *Dreissena polymorpha* (Pallas, 1771), species included among the world's worst invasive species. Some have become naturalized: three brackish and marine species, six freshwater, and twelve terrestrial. The increase in exchange of goods, services, and transport has assisted in the transfer of species from distant places, as has intentional or unintentional introduction of species of economic importance (*M. galloprovincialis*, *Crassostrea gigas* (Thunberg, 1793), *C. sikamea* (Amemiya, 1928)), without consideration of the epibionts, endobionts, and endoparasites that may also be introduced. Effective strategies must be developed to minimize the potential impact of biological invasions and raise public awareness of the problem; this must include the rigorous application of more stringent regulations.

Additional Keywords: exotic, freshwater, terrestrial mollusks, marine, mollusks, economic and biological risks

INTRODUCTION

Biological contamination in the world has increased markedly since 2000 (Crocetta et al., 2013), Pimentel et al. (2001) estimated that some 480000 species have been introduced around the world throughout the history of humankind, and this is of great concern. The effects that alien species may have in ecosystems (Carlton, 1999) and in their interaction with native

organisms are poorly understood; however, we face loss of diversity (Reyna et al., 2013) of formerly diverse ecosystems (Cowie, 1998, 2001; Cowie and Robinson, 2003; López-López et al., 2009). It may be possible that endemic species are the most vulnerable, although unfortunately, knowledge of the diversity and abundance of much of the world's fauna remains unsatisfactory. In Mexico, where it is estimated that 75 % of brackish and marine species are known, it is suggested that 17 % of the Pacific species, and 15% of those in the Gulf of Mexico and the Caribbean Mexican coast are endemic (Castillo-Rodríguez, 2014). On the other hand, fewer than 35 % of the native non-marine mollusks are known and 85% of the Mexican territory is in need of exploration (Thompson, 2011).

In the case of the introduction pathways at global level, marine vectors are well documented. Mexico has a navigation infrastructure that facilitates the introduction of alien species; human activities on the continental margins, and in the bays and estuaries of the coastal zone, have evolved since the 16th century and are now part of an impressive network of global marine traffic. Currently there is the threat of climate change, which will undoubtedly alter the structure and composition of native communities. This will also alter the functioning of ecosystems and become a stressor that will further increase the risk of biological invasions in marine and non-marine systems. The effects of climate change on the environment will include substantial impact on native species. Given the increase in threats to the native fauna, inventories of exotic species become the foundation for future actions, including the control and eradication of invasives (Mendoza et al., 2014). This article offers a review of the brackish-marine and non-marine introduced mollusks in Mexico, constituting the first national inventory of this type elaborated in Mexico; it also determines the naturalized species at the national level. We examine potential vectors and recommend measures that may help prevent the entry of additional alien organisms and that could help control and serve as essential protective measures for the fauna and the environment at the national level in Mexico.

EARLY RECORDS OF INTRODUCED MOLLUSKS IN MEXICO

In relation to introduced non-marine mollusks, *Cornu aspersum* (Müller, 1774) (as *Helix aspersa* Müller, 1774) was detected in Mexico by Alexander Humboldt between 1803 and 1804 (Martens 1890–1901); and it was recorded by Pilsbry (1891) in Mexico City. It was also located in Jalal, Guanajuato, and other unspecified sites (Martens 1890–1901). The species became a pest in gardens throughout Mexico City (Ancona, 1947) and was later recorded at Chapultepec, and in mountains between Mexico City and the city of Cuernavaca (Jacobson, 1952). Baker (1925) mentioned the presence of *Phyllocaulis gayi* (Fischer, 1871) in Mazatlán, Sinaloa. Andrews and Dundee (1987) stated for the first time the problems caused by the slug *Sarasinula plebeia* (Fischer, 1868) in Chiapas (1980) and Veracruz (1981), and Naranjo-García et al. (2007) reviewed the distribution of the family Veronicellidae nationwide, with particular reference to *Sarasinula plebeia* (= *Sarasinula dubia* (Semper, 1885)). As for other introduced slugs, Cockerell (1923) recorded *Limax flavus* (Linnaeus, 1758) (as *Limax flavus* Linnaeus, 1758) with numerous individuals or populations in Mexico City. After that, Baker (1930) found various European slugs (*Limax maximus* Linnaeus, 1758 in Desierto de Los Leones to Cuajimalpa; *L. flavus* in Huachinango, Puebla; *Deroceras laeve* (Müller, 1774) (aphallic) in Desierto de Los Leones and Necaxa; *D. laeve* (phallic) (Müller, 1774) in Cuajimalpa and San Juan Teotihuacan; and *Milax gagates* (Draparnaud, 1801) in Desierto de Los Leones. The Cuban species *Zachrysia auricomya havanensis* Pilsbry, 1894 was recorded in Yucatan (Bequaert and Clench, 1936) and *Vallonia excentrica* Sterki, 1893 was found by Joshua L. Baily Jr. in Cuernavaca (Pilsbry, 1948).

The freshwater clam *Corbicula fluminea* (Müller, 1774) (as *Corbicula manilensis* (Philippi, 1844)) was recorded in Baja California, northwestern Mexico (Fox, 1970) and Hillis and Mayden (1985) summarized its distribution along the coastal areas of Pacific and in the State of Tamaulipas; it was later recorded in Lake Catemaco, southern Veracruz (Torres-Orozco and Revueltas-Valle, 1996). The freshwater snail *Melanoides tuberculata* (Müller, 1774) was found in the vicinity of Veracruz in 1973 (Abbott, 1973), and its presence in Mexico was confirmed in 1975 by Pointier and McCullough (1989). More details of its distribution in Mexico have subsequently emerged (Contreras-Arquieta, 1998; Contreras-Arquieta and Contreras-Balderas, 2000; Contreras-Arquieta, et al. 1995). The first record of *Tarebia granifera* (Lamarck, 1822) was at Lake Catemaco, Veracruz (Naranjo-García et al., 2005), and other foci were later found in northern Veracruz State (López-López et al., 2009), in southern Oaxaca State, and in the Lacandona Forest, Chiapas (Naranjo-García non-published data); it was later recorded from 11 lakes of three municipalities in the State of Tabasco (Rangel-Ruiz et al., 2011).

The terrestrial species *Rumina decollata* (Linnaeus, 1758) was recorded in 1993 in the States of San Luis Potosí and

Tamaulipas (Correa-Sandoval, 1993, 1998; Correa-Sandoval and Rodríguez, 2002), and soon afterward in Nuevo Leon (Correa-Sandoval 1999b; Correa-Sandoval and Rodríguez, 2005; Correa-Sandoval et al., 2007). *Huttonella bicolor* (Hutton, 1834) (as *Gulella bicolor* (Hutton, 1834)) was collected at the archaeological site El Tajín, Veracruz (Correa-Sandoval, 1999a, 2000).

In relation to marine mollusks introduced into Mexican waters, Hendrickx (1980) and Salgado-Barragán and Toledano (2006) provided data from specimens observed *in situ* and preserved in the Invertebrate Collection (EMU) of Unidad Académica of Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. There are also other published records: for example, Okolodkov et al. (2007) and Ortiz-Arellano and Salgado-Barragán (2012). According to Carlton (1999), the diversity and abundance of exotic and invasive marine species at worldwide level are still poorly known; this is certainly true for Mexico, where lack of awareness of the presence of exotic species is compounded by unfamiliarity of their effects on the ecosystems.

MATERIALS AND METHODS

The present compilation was assembled based on records of mollusks deposited in: Colección Nacional de Moluscos (National Collection of Mollusks), Instituto de Biología, Universidad Nacional Autónoma de México; database of the Invertebrate Zoology division of the Florida Museum of Natural History, FLMNH; the Unidad Académica of Mazatlán of the Instituto de Ciencias del Mar y Limnología (ICMyL-MAZ, UNAM); the literature; field observations by the authors and/or other specialists; a list of organisms coming from Mexico and intercepted at customs upon arrival in the USA; and additional information provided by David Robinson (letter to E. Naranjo-García, 4 September 2014). In certain cases, where the literature is very extensive, the first and the most recent articles or references were selected. Acronyms used are: CNMO, Colección Nacional de Moluscos, Universidad Nacional Autónoma de México; CM, Carnegie Museum of Natural History, Pittsburgh; FLMNH, database of the Florida Museum of Natural History, Gainesville; EMU, Colección de Invertebrados, Unidad Académica de Mazatlán del Instituto de Ciencias del Mar y Limnología.

RESULTS

In total, 56 species of exotic-invasive mollusks from the classes Bivalvia and Gastropoda have been so far introduced into Mexico, whether intentionally or not: 15 brackish-marine, 10 freshwater, and 31 terrestrial mollusks (Tables 1, 2, and 3). Of these, 36 % came from Europe and the Mediterranean (the majority are terrestrial mollusks), 18 % from Asia-Australia-New Caledonia

Table 1. Exotic estuarine marine mollusks recorded in Mexico: place of origin, references or sources, means of introduction (vector), and habitat; * = Naturalized.

Family	Species	Origin	Source	Vector	Habitat
Arcaidae	<i>Anadara transversa</i> (Say, 1822)*	Northwestern Atlantic from Cape Cod to Texas, USA.	Laguna de Taniahua, Veracruz, (García-Cubas, 1969; Abbott, 1974); Tamaulipas shore (Correa-Sandoval and Rodríguez-Castro, 2013)	Ballast water/ escorting fauna of economically important species	Estuarine-marine
Mytilidae	<i>Arcautula senhousia</i> (Benson in Cantor, 1842)	Asia (Japan and China)	Estero de Punta Banda, Baja California (Cohen, 2005)	Ballast water/ Aquaculture	Estuarine-marine
Terididae	<i>Bankia destructa</i> Clench and Turner, 1946	Caribbean	Laguna Caimanero, Sinaloa (Hendrickx, 1980)	Regional and cosmopolitan distribution hydraulic transport	Estuarine-marine
	<i>Bankia zeteki</i> Bartsch, 1921	Caribbean (Panama and Colombia)	Teacapan, Mazatlán, Sinaloa (Hendrickx, 1980)	Regional and cosmopolitan distribution hydraulic transport	Estuarine-marine
Pyramidelidae	<i>Boonea bisuturalis</i> (Say, 1822)	Delaware, Canada and Massachusetts, New York, USA	Arrecife Lobos, Veracruz (De la Cruz and González, 2006)	Aquaculture (polluted oysters)	Estuarine-marine
Littorinidae	<i>Cenchritis muricatus</i> (Linnaeus, 1758)*	Gulf of Mexico, Caribbean, the Antilles, Costa Rica, Cuba, Panama, Puerto Rico, Venezuela	Gulf of California (Carlton 1992, Bishop, 1992; Chaney, 1992)	Regional and cosmopolitan distribution hydraulic transport	Marine
Ostreidae	<i>Crassostrea gigas</i> (Thunberg, 1793)*	Japan and Korea	Bahía San Quintín, Baja California (Islas-Olivares, 1975)	Aquaculture	Marine
	<i>Crassostrea sikamea</i> (Anemiyá, 1928)	China	San Quintín, Baja California (Cáceres-Martínez et al., 2012)	Aquaculture and coastal transports	Marine
Mytilidae	<i>Geukensia demissa</i> (Dillwyn, 1817)	North-eastern America	Estero Punta Banda, Baja California (Torrelin et al., 2005)	Aquaculture and coastal transports	Estuarine
Dreissenidae	<i>Mytilopsis adamsi</i> Morrison, 1946	Native to tropical west Pacific of Central America	Estero Urtas, Mazatlán (Salgado-Barragán and Toledano-Granados, 2006)	Aquaculture	Estuarine
Mytilidae	<i>Mytilus galloprovincialis</i> Lamarek, 1819	Mediterranean, Black sea and Adriatic sea	Bahía de Todos los Santos, Baja California (Curiel-Ramírez and Cáceres-Martínez, 2009)	Aquaculture	Estuarine-marine
	<i>Perna perna</i> (Linnaeus, 1758)	Indo-Pacific Region	Gulf of Mexico, Veracruz (Hicks and Tunnell, 1995); Tamaulipas coast (Correa and Rodríguez, 2013)	Ballast water	Estuarine-marine
Terididae	<i>Teredo bartschi</i> Clapp, 1923	South of Carolina to Texas, USA. and Bermuda	Laguna Caimanero, Sinaloa (Hendrickx, 1980)	Regional and cosmopolitan distribution hydraulic transport	Marine
	<i>Teredo navalis</i> Linnaeus, 1758	Mediterranean-Europe -Western Atlantic	Cancun, Quintana Roo, FLMNH year 1957-CN: 349169-Mollusca; Bahía de Campeche (López-Garrido, 2008)	Ballast water	Estuarine-marine
Semellidae	<i>Theora lubrica</i> Gould, 1861	Asia (South of Japan to Singapur and Indonesia)	Tijuana-Ensenada, Baja California (Carpizo-Ituarte and Rodríguez, 2009)	Ballast water	Estuarine-marine

* Naturalized

(several estuarine/brackish- marine and some freshwater species), 46 % from different regions of the planet (Table 4), with the place of origin of several being uncertain.

Most of the brackish and marine species (Table 1) belong to the families Mytilidae and Teredinidae (Bivalvia). Among the freshwater mollusks (Table 2), gastropods are the dominant group, in particular species in the families Ampullariidae, Thiaridae, and Planorbidae. Most of the terrestrial mollusks (Gastropoda) (Table 3) belong to the family Helicidae, followed by the Agriolimacidae, the Limacidae, the Subulinidae, and the Vallonidae. The species that have been recorded only once are: *Theora lubrica* Gould, 1861 (marine), *Helisoma duryi* (Wetherby, 1879) (as *Planorbella duryi* (Wetherby, 1879)) (freshwater), and *Phyllocaulis gayi*, *Ceciloides acicula* (Müller, 1774), *Arion circumscriptus* Johnston, 1828, *Vallonia costata* (Müller, 1774), *Zachrysia auricomya havanensis*, and *Cantareus apertus* (Born, 1778) (as *Helix aperta* Born, 1778) (terrestrial).

DISCUSSION

MARINE MOLLUSKS

The ecosystems that now are home to exotic mollusks are vulnerable to changes in their composition, regardless of whether those mollusks were introduced inadvertently or for commercial purposes. Especially threatening are those species that have been restricted to environments disturbed either naturally or by human intervention, as is the case of brackish and marine mollusks such as *Mytilus galloprovincialis* Lamarck, 1819 (Mytilidae). *Mytilus galloprovincialis*, originally from the Mediterranean, Black Sea and Adriatic Sea, has been categorized as one of the 100 worst invasive alien species of the world. Despite this, the species is cultivated for food in the states of Baja California Norte and Sur, and this is without any knowledge of its ecological impact on the native species. Populations of the mussel *Perna perna* (Linnaeus, 1758) are distributed from Texas to southern Veracruz State, Mexico (Hicks and Tunnell, 1993, 1995; McGrath et al., 1998), and Hicks et al. (2001) consider that its occurrence on Mexican coasts should be carefully monitored.

Mussels and shipworms can survive tough conditions in variable estuarine and marine environments, as well as in sheltered sites that may be favorable to their development and dispersal: they are adapted to this survival by their sessile habit, their filter feeding, and their modes of reproduction, growth, and morphological protection ((McDonald and Koelm, 1988; Turner, 1966; Tuente et al., 2002; Petes et al., 2007; Didziulis, 2007).

The shipworms, such as *Teredo navalis* Linnaeus, 1758, bore into submerged wood substrata all over the world, and there are few records of the species in Mexico. López-Garrido (2008) recorded the species from sunken boats in the state of Campeche, in the southern Gulf of Mexico. There are also references from the early 1900s (Dublán

and Lozano, 1901; Mariscal, 1902) regarding requirements of the asphalt composition in Submarine Telegraph cables between the port of Veracruz and Campeche in order to avoid damage caused by the "marine worm", *T. navalis*. More recently, there are checklists, reports and theses records of its presence in estuaries on the Mexican coast of the Gulf of Mexico, such as the Tampamachoco Lagoon, Veracruz (without reference code), where it has been an element of the epibiosis on the mangrove *Rhizophora mangle* Linnaeus, 1753 since 1980.

Oysters of Asian origin, *Crassostrea gigas* (Thunberg, 1793) and, more recently, *C. sikamea* (Amemiya, 1928), are cultivated in Baja California Norte and Sur in Mexico. Sessile oysters adhering by cementing to any hard substratum, together with the large accompanying fauna on the surface of their shells, represent a potential risk to wildlife; hence, a study of their ecological impact would be most important. *Crassostrea gigas* exists as an exotic species on the southern Pacific coast and, since uncontrolled introduction is possible through ballast water and aquaculture practices, it might also be expected to eventually be introduced along the southern Gulf of Mexico, in locations as Veracruz State.

Anadara transversa (Say, 1822), a clam from the northwestern Atlantic, is considered a non-invasive exotic species. It was recorded in Tamiahua lagoon, Veracruz by García-Cubas (1969) and Abbott (1974). Although there are no recent records of substantial living populations, abundant disjointed valves have been reported.

Theora lubrica Gould, 1861, originally from Asia, is considered as one of the most important invasive species in Europe (Balena et al., 2002). According to Steneck and Carlton (2001), it is one of the 15000 species that have been transported across the world in ballast water. It is recorded from Baja California Norte, where it possibly arrived secondarily introduced from San Francisco Bay, USA; it can be considered a potentially invasive species for the Pacific States of Mexico.

There are fewer records of exotic marine gastropods species in Mexico than of exotic bivalve species. Among these gastropods is the pyramidellid *Boonea bisuturalis* (Say, 1822), a native of the northern coast of the Atlantic (Canada and USA) that feeds on the body fluids of invertebrates (Fretter and Graham, 1949; 1962; Fretter, 1951), including polychaetes, gastropods, and bivalves, and minor groups such as polyplacophorans and some echinoderms (Robertson and Orr, 1961). The Mexican coast of the Gulf of Mexico houses marine resources that include the Eastern Oyster *C. virginica* (Gmelin, 1791), which represents 90% of the catch produced along that coast (Cáceres-Martínez and Vásquez-Yeomans, 2013). Despite studies on diseases and ectoparasites of *C. virginica* in Mexico (Aguirre-Macedo et al., 2007; Cáceres-Martínez and Vásquez-Yeomans, 2013), a study of non-native endo- and ecto-parasites of mollusks in the coastal lagoons and coral reefs of the southern gulf is still lacking. However, *B. bisuturalis* (Say, 1822) has been registered by De la Cruz and González-Gándara (2006)

Table 2. Exotic freshwater mollusks recorded in Mexico, where are shown: place of origin, references or source, means of introduction (vector), habitat and impact with regard to the damage they may cause; * = Naturalized, ** = data provided by David G. Robinson.

Family	Species	Origin	Source/ record CNMO	Vectors	Habitat	Impact
Ampullariidae	<i>Pomacea canaliculata</i> (Lamarck, 1822)*	Argentina, South America	Thiengo et al., 1993; Campos et al., 2013, Rawlings et al., 2007	Aquarium trade/ food trade (Rawlings et al., 2007)	Diverse bodies of water w/ abundant vegetation	Harmful
	<i>Pomacea diffusa</i> Blume, 1957**	Santa Cruz, Bolivia, South America	Specimens caught at the USA and Mexico border, place of dwelling unknown (Robinson, 2014, pers. comm.)	Aquarium trade / food trade	Diverse bodies of water w/ abundant vegetation (Covie et al., 2006)	Potential pest
	<i>Pomacea flagellata</i> (Say, 1829)*	Gulf of Mexico states in Mexico	Colima, State of Morelos (CNMO 498, 1731, 2007)	Unknown reasons for introduction	Diverse bodies of water plus cenotes and micro-cenotes (Negrete Yankelevich, 1998)	Potential pest
Thiaridae	<i>Tarebia granifera</i> (Lamarck, 1822)*	Madagascar India, Asia (Pace, 1973)	Naranjo-García et al., 2005. Chiapas, Michoacán, Oaxaca, Tabasco, Veracruz (CNMO 1616, 1707, 2051, 2191, 2557, 2746, 2751, 2831, 2832, 3240, 3295, 3315, 3348, 3467, 3507, 3562, 3693, 3700, 3701, 3749, 3810, 3914)	Aquarium trade / possible transport by birds (Naranjo-García non published data)	Diverse bodies of water, ca. 1.5 m of depth (Chianotis et al., 1980; Appleton et al., 2009)	Pest

(Continued)

Table 2. (Continued)

Family	Species	Origin	Source/ record CNMO	Vectors	Habitat	Impact
Lymnaeidae	<i>Melanooides tuberculata</i> (Müller, 1774)*	Africa, Asia (Pace, 1973)	Abbott, 1973; Contreras-Arquieta and Contreras Balderas, 2000, Baja California Sur, Coahuila, Chiapas, Colima, Guerrero, Jalisco, Michoacán, Oaxaca, Quintana Roo, San Luis Potosí, State of Morelos, Tabasco, Tamaulipas, Veracruz, Zacatecas (CNMO 18, 288, 293, 296, 300, 420, 430, 431, 442, 580, 583; Mexico City: CNMO 683, 709-718, 725, 726, 813, 1169, 1236, 1088, 1376, 1617, 1678, 1680, 1683, 1699, 1714, 1867, 1926, 1954-57, 2020, 2050, 2052, 2055-56, 2058, 2061, 2071, 2168-71, 2174-76, 2187, 2189, 2192-93, 2206, 2213-15, 2478, 2554-58, 2561, 2565, 2639, 2753, 2763, 2832, 3086, 3088, 3203, 3256, 3258, 3260, 3301, 3384, 3481, 3534, 3552, 3764, 3880-82)	Aquarium trade	Diverse bodies of water	Pest
	<i>Radix auricularia</i> (Linnaeus, 1758)*	Europe, North of Asia	Böhm, 1983, Hidalgo (CNMO 2218)	Aquarium trade?	Lakes w/ abundant vegetation abundant, old river arms (Welter-Schultes, 2012)	Unknown if is a potential pest
Planorbidae	<i>Ameriauna carinata</i> (H. Adams, 1861)**	Australia	Specimens caught at the USA-Mexico border, place of dwelling unknown (Robinson, 2014, pers. comm.)	Aquarium trade?	River shores, temporal bodies of water w/ abundant vegetation	Unknown if is a potential pest

(Continued)

Table 2. (Continued)

Family	Species	Origin	Source/ record CNMO	Vectors	Habitat	Impact
	<i>Helisoma duryi</i> (Wetherby, 1879)	Florida	Mexico City (CNMO 758)	Aquarium trade?	Shallow water bodies near to human beings	Can reach abundant populations, unknown if is a potential pest
Cyrenidae	<i>Corbicula fluminea</i> (Müller, 1774)*	Asia	Hillis and Mayden, 1985, Contreras-Arquieta et al., 1995, Colima, Chiapas, Chihuahua, Durango, Jalisco, Michoacán, Nayarit, Oaxaca, San Luis Potosí, Sonora, Veracruz, Zacatecas (CNMO 299, 301, 314, 440, 443, 495, 689, 771, 799, 1163, 1679, 1681-82, 1684-85, 1690, 1692, 1700, 1705, 1720, 1735, 1857, 2097, 2164-67, 2597, 2840, 2827, 2940, 2942, 3065, 3177, 3179, 3284, 3385, 3773, 3847)	As food	Diverse bodies of water	Pest
Dreissenidae	<i>Dreissena polymorpha</i> (Pallas, 1771)*	Black sea and Caspian Sea (Leentvaar, 1971)	Veracruz (CNMO 3257, 6060)	Ballast water	Rivers and lakes	Potential pest in Mexico

Table 3. Exotic terrestrial mollusks recorded in Mexico: place of origin, references or sources, means of introduction (vector), habitat and impact with regard to the damage they may cause; * = Naturalized, ** = data provided by David G. Robinson.

Family	Species	Origin	Reference/Source	Vector	Habitat	Impact
Veronicellidae	<i>Sarasinula plebeia</i> (Fischer, 1868)*	New Caledonia	Andrews and Dundee, 1957; Naranjo-García et al., 2007. Colima, Chiapas, Jalisco, Oaxaca, Querétaro, San Luis Potosí, Sinaloa, State of Morelos, Tabasco, Veracruz, Yucatán (CNMO 63, 173, 271, 414, 553, 556, 559, 561, 635 - 641, 1072, 1656, 1727, 1762, 1763, 4425, 4539, 4933, 4934, 4936, 4937, 4938, 5013, 5014)	Plants transportation	Diverse habitats reaching 1000 m of altitude (Caballero et al., 1991)	Pest
Punctidae	<i>Phyllocaulis gagi</i> (Fischer, 1871)	South America (Chile)	Baker, 1925	Plants or goods transportation	Damp forests (Stuardo and Vargas-Almonacid, 2000)	Unknown if is a potential pest
	<i>Paralaana servilis</i> (Shuttleworth, 1852)*	Canary Islands/ Oceania? (Rumi et al., 2010)	Rivera-García, 2013, Mexico City (CNMO 2803, 3224, 4408, 4409, 4410, 4411, 4412, 4413, 4414, 4416, 4429, 4715)	By human activities (Thompson, 2011)	Diverse habitats, pine and olive forests, disturbed sites and gardens (Štámol and Kletečki, 2009; Welter-Schultes, 2012)	Unknown if is a potential pest
Milacidae	<i>Milax gagates</i> (Draparnaud, 1801)	W Mediterranean	Baker, 1930, Roth and Sadeghian, 2003, Mexico City, State of Morelos (CNMO 2211, 3449, 5042)	Plants or goods transportation	Cultivated fields, forests and shrub areas (Welter-Schultes, 2012)	Pest
Boettgeriidae	<i>Boettgerilla pallens</i> Simroth, 1912	W Caucasus	Mexico City, Puebla (CNMO 1520, 5554)	Plants transportation	Damp forests, gardens and disturbed sites. It lives deeply buried in the soil (South, 1992, Mc Donnell et al., 2014, Welter-Schultes, 2012)	Garden and Green houses in the United Kingdom (Welter-Schultes, 2012)
Arionidae	<i>Arion circumscriptus</i> Johnston, 1928*	NW and Central Europe to N Italia	Mexico City (CNMO 020, 3470)	Plants transportation	Cold and damp forests, crops fields and gardens (Welter-Schultes, 2012)	Unknown if is a potential pest

(Continued)

Table 3. (Continued)

Family	Species	Origin	Reference/Source	Vector	Habitat	Impact
Agriolimnidae	<i>Arion intermedius</i> Normand, 1852**	Europa	Specimens caught at the USA and Mexico border, place of dwelling unknown (Robinson, 2014, pers. comm.)	Plants transportation	Grass fields and rubbish sites (South, 1992)	Potential pest
	<i>Deroceras incalescens</i> Reise, Hutchinson, Schunack, and Schlitt, 2011	Great Britain (Reise, Hutchinson, Schunack and Schlitt, 2011)	Mexico City (CNMO 3451) Specimens caught at the USA and Mexico border, place of dwelling unknown (Robinson, 2014, pers. comm.)	Forage cargos, materials for Green houses, nurseries, gardens and commercial vegetables (Reise et al., 2006)	Shaded places, with human influence (Welter-Schultes, 2012)	Pest
	<i>Deroceras laeve</i> (Müller, 1774)*, phallic form	Paleartic from Denmark (Thompson, 2011)	Martens, 1898: 348; Baker, 1930. Chiapas, Michoacán, State of Morelos, Durango, Mexico City (CNMO 59, 281, 284, 286, 298, 306, 3154, 4019, 4430)	Plants transportation	Diverse habitats: from tropical to subpolar (Welter-Schultes, 2012)	Pest
	<i>Deroceras laeve</i> (Müller, 1774)*, aphallic form	Paleartic	Martens, 1898; Baker, 1930 (Desierto de los Leones, Necaxa). Coahuila, Jalisco, Michoacán, San Luis Potosí, State of Mexico, Veracruz (CNMO 278, 279, 627, 1080, 1081, 1635, 1637, 2672, 3153, 3390, 3394, 3447)	Plants transportation	In Spain close to human surroundings; in crop fields and at side of roads (Castillejo, 1998)	Pest
Limacidae	<i>Deroceras reticulatum</i> (Müller, 1774)*	Europe	Mexico City, State of Mexico (CNMO 7, 21, 435, 560, 3264, 3413, 3420, 3437, 3440, 3442, 3717)	Plants transportation	Near to human surroundings (Welter-Schultes, 2012).	Serious Pest
	<i>Lehmannia valentiana</i> (Ferussac, 1821)*	Iberic Peninsula	Aguascalientes, Coahuila, Mexico City, Michoacán, Sinaloa, State of Mexico, Veracruz (CNMO 282, 287, 289, 291, 292, 294, 305, 306, 734, 1068, 1768, 2210, 3151, 3231, 3353, 3393, 3404, 3439, 3452, 3556)	Plants transportation	Near to human surroundings, in Green houses (Kerney and Cameron, 1996; Welter-Schultes, 2012)	Pest

(Continued)

Table 3. (Continued)

Family	Species	Origin	Reference/Source	Vector	Habitat	Impact
Valloniidae	<i>Limacus flavus</i> (Linnaeus, 1758)*	Europe	Baker, 1930 (Puebla, Huachinango) Chihuahua, Jalisco, Mexico City, State of Mexico (CNMO 557, 1729, 1732, 3158, 3354, 3396, 3398, 5098)	Plants transportation	Near to human surroundings, wet walls of old buildings, and basements (Welter-Schultes, 2012)	Pest (possibly because of its numerous egg masses 40-60)
	<i>Linax maximus</i> Linnaeus, 1758*	Europe	Desierto de Los Leones and Mexico City, State of Mexico (CNMO: 29, 113, 3155, 3352, 3453, 3485, 3492, 3860)	Plants transportation	Sheltered damp places, at night climb trees; in compost, gardens, cemeteries, etc. (Welter-Schultes, 2012)	Potential Pest (Welter-Schultes, 2012)
	<i>Vallonia costata</i> (Müller, 1774)	N Africa and Europe to Central Asia	Mexico City (CM 143801, CNMO XXX)	Plants transportation	Among grasses, at side of roads (Hubricht, 1985); open and dry sites, around calcareous soil, rocky places and dunes of sand, scarce shaded places (Welter-Schultes, 2012).	Unknown if is a potential pest
Ferussaciidae	<i>Vallonia excentrica</i> Sterki, 1893	Europe/ North America	Cuernavaca, State of Morelos (Pilsbry, 1948); Mexico City (ENG 022, 188, 195, 237)	Plants transportation	Among grasses, at side of roads (Hubricht, 1985); open and dry sites rocky places and dunes of sand (Welter-Schultes, 2012)	Unknown if is a potential pest
	<i>Cecilioides acicula</i> (Müller, 1774)	Europe	Mexico City (ENG 236)	Plants transportation	Two meters' depth into sub- soil, frequent around 20 -40 cm., in rocky areas among leaf litter, roots, or river detritus. Non found alive (Welter-Schultes, 2012)	Potential pest

(Continued)

Table 3. (Continued)

Family	Species	Origin	Reference/Source	Vector	Habitat	Impact
Subulinidae	<i>Opeas hannense</i> (Rang, 1831)**	Cape Verde, Village of Hann (Rang, 1831; Pilsbry, 1906)	Specimens caught at the USA and Mexico border, place of dwelling unknown (Robinson, 2014, pers. comm.)	Plants transportation	Diverse tropical and subtropical habitats; below rocks, plant detritus and humus (Pilsbry, 1946)	Unknown if is a potential pest
	<i>Subulina octona</i> Brugnière, 1789	South America (possibly) (Thompson, 2011)	Veracruz and Tabasco (Martens, 1890-1901). Sinaloa, State of Morelos, State of Mexico (CNMO 1164, 1664, 1758, 2482). Chihuahua, Coahuila, Durango, San Luis Potosí, Hidalgo, Jalisco, Puebla, State of México (CNMO 297, 316, 787, 1069, 1074, 1076, 1386, 1686, 1738, 1766, 1993, 2939, 2941, 2943, 3293, 3397, 3399)	Possibly with plants (Pilsbry, 1946)	Found frequently in nurseries	Unknown if is a potential pest
	<i>Rumina decollata</i> (Linnaeus, 1758)*	Mediterranean	North of Veracruz (Correa-Sandoval, 1999)	Plants transportation	Arid surroundings (De Francesco and Lagiglia, 2007). Abundant in crop fields (Correa-Sandoval, 1993)	Could impact populations of native mollusks
Streptaxidae	<i>Huttonella bicolor</i> (Hutton, 1834)	Mirzapur (Hutton, 1834; Thompson, 2011), according to J.C. Bequaert from Africa (van der Schalie, 1948)	North of Veracruz (Correa-Sandoval, 1999)	Possibly by plants transportation	Near human surroundings (Amundale and Prashad, 1920; Pilsbry, 1926), gardens, crop fields, secondary forests (Vermeulen, 2007).	Could impact populations of native mollusks
Oxychilidae	<i>Oxychilus draparnaudii</i> (Beck, 1837)*	Europe	Mexico City [Distrito Federal] (CNMO 015, 308, 433, 514, 518, 525, 829, 2816, 2817, 2818, 3225, 3230, 3721, 3726, 3730, 3857, 3858, 3862) (CM 143802)	Plants transportation	Damp areas, below leaf litter, rocks in semi open and open environments; gardens, green houses near humans (Welter-Schultes, 2012)	Could impact populations of native mollusks (predator)

(Continued)

Table 3. (Continued)

Family	Species	Origin	Reference/Source	Vector	Habitat	Impact
Camaenidae	<i>Zachrystia auricomya</i> <i>havanensis</i> Pilsbry, 1894	Cuba, La Habana.	Quinta in Mérida, Yucatán (Bequaert and Clench, 1936: 64)	Plants transportation	Dry sites with scarce shade, loose rock places, gardens; low shady places with scarce height (Pilsbry, 1929)	Unknown if is a potential pest; potential vector of veterinary diseases
Gastrodontiidae	<i>Zenitoides arboreus</i> (Say, 1816)*	Philadelphia, Pennsylvania, USA	Puebla, Necaxa (Baker, 1930); Mexico City (ENG 24, CNMO 3229)	Plants transportation	Damp forests (Welter Schultes, 2012), below bark, tiles, rocks; eats sugar cane roots (Pilsbry, 1946:483)	Potential pest (Hawaii a pest) (Hollingsworth and Armstrong, 2003)
Helicidae	<i>Cantareus apertus</i> (Born, 1778)	Africa and Europe, Mediterranean (Roth and Chivers, 1980).	Mexico without more data (Roth and Sadeghian, 2003: 35)	Plants transportation	Warm and dry sites (Marasco and Murciano, 1986) among shrubs, near crop fields, gardens (Welter-Schultes, 2012).	Potential pest
	<i>Cornu aspersum</i> (Müller, 1774)*	Europe	Recorded by Humboldt around 1803 (Martens, 1890-1901); Mexico City (Pilsbry, 1891); Martens, 1890-1901), Mexico City, State of México, Tlaxcala, Puebla, Hidalgo, Michoacán, Veracruz, Chiapas (CNMO 22, 24, 34, 79, 153, 161, 269, 272, 280, 307, 330, 408, 436, 437, 438, 439, 444, 445, 453, 460, 506, 517, 647, 649, 777, 779, 780, 781, 810, 1242, 1331, 1746, 1747, 1748, 1749, 1750, 1751, 1756, 1812, 1997, 2340, 2622, 2760, 2805, 3083, 3182, 3232, 3343, 3632, 3640, 3643, 3527, 3714, 3716, 3728)	Plants transportation	Dry sunny places, with scattered vegetation, or near the sea (Marasco and Murciano, 1986)	Pest in crops, gardens and orchards (possibly for the numerous eggs)

(Continued)

Table 3. (Continued)

Family	Species	Origin	Reference/Source	Vector	Habitat	Impact
	<i>Theba pisana</i> (Müller, 1774)**	Mediterranean	Specimens caught at the USA and Mexico border, origin unknown (Robinson, 2014 pers. comm.)	Plants transportation	Near the coast, Sandy areas, warm environments; goes dormant under the sun (Welter-Schultes, 2012)	Pest, possibly because the numerous eggs (40-80) (Welter-Schultes, 2012)
	<i>Eobania vermiculata</i> (Müller, 1774)**	Mediterranean	Specimens caught at the USA and Mexico border, origin unknown (Robinson, 2014 pers. comm.)	Plants transportation	Diverse dry environments; near the sea or field crops (Welter-Schultes, 2012)	Potential pest (possibly by the number of eggs 60-80) (Welter-Schultes, 2012)
	<i>Otala lactea</i> (Müller, 1774)**	SW Europe, Morocco	Specimens caught at the USA and Mexico border, origin unknown (Robinson, 2014 pers. comm.)	Plants transportation	Around shrubs of rocky areas; open spaces (Welter-Schultes, 2012)	Potential pest
Cochlicellidae	<i>Priocella barbara</i> (Linnaeus, 1758)**	Mediterranean	Specimens caught at the USA and Mexico border, origin unknown (Robinson, 2014 pers. comm.)	Plants transportation	Near the sea, dry and Sandy, or sand dunes covered with grasses (Welter-Schultes, 2012)	Potential pest [in cultivated grass]
Bradybaenidae	<i>Bradybaena similaris</i> (Férussac, 1822)**	Eastern Asia, China, SE Asia, Japan (Schileyko, 2004)	Specimens caught at the USA and Mexico border, origin unknown (Robinson, 2014 pers. comm.)	Plants transportation	In disturbed places, forests, gardens, near urban environments (Vermeulen and Whitten, 1998)	Potential pest [pest in grape orchards]
Lauriidae	<i>Lauria cylindracea</i> (Da Costa, 1778)**	W Europe and Mediterranean	Specimens caught at the USA and Mexico border, origin unknown (Robinson, 2014 pers. comm.)	Plants transportation	In forests, among wet rocks. In Crimea abundant in semi-dry areas. In Portugal in moss; below rocks, leaf litter, bark damp shady places (Welter-Schultes, 2012)	Unknown if is a potential pest

Table 4. Species introduced in Mexico per region of origin and percent which they represent.

Origin	No.species	Percentage
Europe	15	26.70
Asia	8	14.20
North America	5	9.00
Mediterranean	5	8.90
Caribbean, Antilles	4	7.00
South America	4	7.00
Africa and Europe	3	5.35
Europe, Asia	2	3.80
W Africa	2	3.80
Australia, New Caledonia	2	3.80
Pacific Central America	1	1.80
Indo Pacific	1	1.80
Bermudas	1	1.80
Eastern Mexico	1	1.80
Africa, Asia	1	1.80
Paleartic	1	1.80
Africa, Europe, Asia	1	1.80
Holarctic	1	1.80

on Lobos Reef, Veracruz. Since this species can survive as an ectoparasite on various invertebrates, it could have been introduced with species such as *C. virginica* as far back as the last century. Its survival would have been favored by the diversity of species that exist on the reef plain of Veracruz; hence, *B. bisuturalis* is likely to be more common in the region than suggested by this single record. Its planktotrophic larvae (Robertson and Maulstovicka, 1979) would enable *B. bisuturalis* to be transferred in ballast water and install itself on various macrobenthic species. Unfortunately, it has not been recorded as introduced to Mexico, perhaps as it is considered by some to be native/naturalized, or because the research has been limited to compilation of a simple checklist. *Boonea* species can seriously affect oyster fisheries and aquaculture (Wilson et al., 1988; Cumming and Alford, 1994), so that establishment large populations of *B. bisuturalis* should be considered as a potential threat to populations of the oysters in Mexico.

Cenchritis muricatus (Linnaeus, 1758) is common in the Caribbean, southern Florida, and the Bahamas (Clench and Abbott, 1942; Abbott, 1954; Trussell, 1997), where it is distributed from the shoreline to a depth of about 3.6 m (Lang et al., 1998; Emson et al., 2002). It withstands desiccation and extreme heat at low tide. It was first recorded in 1992 in the northern part of the Gulf of California.

Diala albugo (Watson, 1886) is a small gastropod of the Indo-Pacific that, as evidenced by its protoconch, possesses a planktotrophic larva (Ponder and De Keyser, 1992). It was included by Aguilar-Estrada et al. (2014) in a checklist of a reef community in Veracruz that consisted mainly of dead specimens. It is not officially registered as introduced in Mexico and, because its identification is difficult, it is not included here nor in Table 1.

Nudibranch gastropods (Heterobranchia) of the genus *Anteaeolidiella* Miller, 2001, *A. foulisi* (Angas, 1864), *A. cacaotica* (Stimpson, 1855), and *A. indica* (Bergh, 1888), recorded in Mexico (Hermosillo et al., 2006; Hermosillo and Gosliner, 2008; Hermosillo, 2009), are not considered here because the systematics of the Aeolidiidae has been undergoing review on the basis of morphological and molecular data (Carmona et al., 2013); those studies will affect the distribution records of previously unrecognized, potentially circumtropical species (Ángel Valdés, personal communication).

FRESHWATER MOLLUSKS

The gastropod *Tarebia granifera* (Lamarck, 1816) from Madagascar, India, and Asia, is ovoviparous, reproducing by parthenogenesis, and matures to a short length (5.5 to 8.0 mm) (Appleton et al., 2009), features that are advantageous in competing with native species following invasion events. In other countries, it can displace native species that display similar habitat requirements, such as those in the genus *Pachychilus* Lea, 1850. In the Caribbean and South America, it displaces and/or regulates populations of species in the genus *Biomphalaria* Preston, 1910 (Pointier and Augustin, 1999; Pointier et al., 1998). Its high reproductive potential allows it to quickly invade bodies of water where it is introduced, and to literally modify its physical conditions; in Mexico, it is considered an invasive species (CONABIO, 2015).

Melanoides tuberculata (O.F. Müller, 1774) (gastropod) and *Corbicula fluminea* (O.F. Müller, 1774) (bivalve), both originating from Asia, are widely distributed in Mexico (Contreras-Arquieta et al., 1995; Contreras-Arquieta, 1998; Contreras-Arquieta and Contreras-Balderas, 1999) and are recognized as invasive species (CONABIO 2015). *Melanoides tuberculata* is ovoviparous and reaches maturity at about 3.5 mm or in about six months (Gutiérrez-Amador et al., 1995; Appleton et al., 2009), which has allowed it to produce large populations very quickly. *Corbicula fluminea* tolerates changes in environmental conditions (Avelar et al., 2014), feeds on suspended material by filtering and through pedal feeding, and influences the abundance of surrounding benthic and pelagic fauna, as well as the organic-matter cycle (Hakenkamp et al., 2001). It may be possible that *C. fluminea* competes for space with native clams of the family Unionidae (Britton and Fuller, 1979).

Pomacea canaliculata (Lamarck, 1822) originally from Argentina, South America (Cowie and Thiengo, 2003), was registered for the first time in the wild in Mexico in 2013. It is presumed that the population in Mexico came from the Colorado River, since it was located in 2005 in that river in Yuma, Arizona, and the Colorado River continues its course in Mexico (Campos et al., 2013). In addition, specimens of apple snails found in California and Arizona have been confirmed to be *P. canaliculata* based on 46 unique mtDNA haplotypes (Rawlings et al., 2007). The presence of non-native apple snails is of great concern due to their ability to spread fast and because they are

recognized as agricultural pests (e.g., in rice fields in Asia). Invasion of exotic apple snails poses a threat to marshland habitats, with the possibility of changes in their diversity and ecological processes, as happened in Laos, South East Asia (Carlsson and Lacoursière, 2005; Rawlings et al., 2007). Apple snails are listed among the world's 100 worst invasive species (Lowe et al., 2000). Its amphibian status and herbivore habits are conducive to its establishment and possibly to its success in environments such as rice fields in Japan, Philippines, China, and other Asiatic countries (Thiengo et al., 1993; Cowie et al., 2006; Rawlings et al., 2007; Ziyuan and Yuansheng, 2012). From the human health point of view, *P. canaliculata*, along with various freshwater or terrestrial molluscan species, is an intermediate host of the low specific host nematode *Angiostrongylus cantonensis* (lung worm); in nature its definite hosts are several species of rodents. *Pomacea flagellata* (Say, 1829), a native of the Gulf of Mexico states, was introduced to the Pacific coast. Its present distribution has facilitated the expansion of the distribution of the snail-eating kite *Rostrhamus sociabilis major* Nelson and Goldman, 1833 by about 900 km into the Pacific region (Hernández-Vázquez et al., 2013). In addition, the "car-rao" *Aramus guarauna dolosus* Peters, 1925 (naturally distributed in the States of Veracruz, Chiapas, and Yucatan) is now found in Laguna del Tule, Barra de Navidad, Jalisco, on the Pacific coast (Hernández-Vázquez et al., 1999; Palomera-García et al., 2006). Dispersals of introduced species may affect native species of birds in the longer term.

Pomacea diffusa Blume, 1957, a species originally from the region of Santa Cruz, Bolivia (Cowie and Thiengo, 2003) has been intercepted in shipments arriving in the USA from an unspecified part of Mexico (David Robinson, personal communication). As Howells et al. (2006) pointed out, "introduced species pose a serious threat to native biodiversity, second only to habitat loss".

The Zebra Mussel *Dreissena polymorpha* (Pallas, 1771) is a great ecological threat (Schloesser and Schmuckal, 2012) and is among the 100 worst invasive species (Lowe et al., 2000). Young specimens have been found at two sites in the State of Veracruz: Río Tonalá, San José, and Río Coatzacoalcas, Napa Creek. (CNMO 3257: Las Choapas. Río Tonalá, San José. Veracruz; and CNMO 6060: Río Coatzacoalcas, Arroyo Napa, Veracruz. So far, these are the first record of the species in Mexico.)

Freshwater species already naturalized in Mexico are: *Pomacea canaliculata*, *Pomacea flagellata* (in the western side of the country where it was not native), *Melanoides tuberculata*, *Corbicula fluminea*, *Tarebia granifera* and *Radix auricularia* (Linnaeus, 1758).

TERRESTRIAL MOLLUSKS

The veronicellid slug *Sarasinula plebeia* (P. Fischer, 1868), originally from New Caledonia (Gomes and Thomé, 2004), is gregarious, able to self-fertilize, and oviparous, attributes that favor its potential as invasive species. The species is thought to have displaced native

counterparts in Central America (Caballero et al., 1991). It is a serious pest of assorted agricultural crops in the southern Catemaco Region, Veracruz (Naranjo-García et al., 2007), and of vanilla in the northern Veracruz State (Velázquez-Montes de Oca et al., 2014).

Phyllocaulis gayi (P. Fischer, 1871) is known to occur in Valdivia, Chile (Thomé, 1971, 1976). However, the species was recorded in the city of Mazatlán, Sinaloa, Mexico in by Baker (1925). Baker suggested that the introduction of the species was probable due to Mazatlán's status as one of the main Pacific ports in Mexico. In 2006, Naranjo-García visited the city of Mazatlán looking for veronicellid slugs, but was unable to confirm the occurrence of *P. gayi* (Naranjo-García et al., 2007). The record of *P. gayi* in Mazatlán was either a misidentification or, if it was present at that time, it did not succeed there.

Cornu aspersum (O.F. Müller, 1774), originally from Europe, tends to be gregarious and to produce large numbers of offspring, attributes that have made it an invasive pest in gardens in Mexico City (Ancona, 1947). They have also destroyed orchards and gardens elsewhere in Mexico (María Villaroel, personal communication), as they have done in other countries (Apablaza, 1984; Cowie, 2000). Introduction may be at the egg stage or as juveniles on imported plants; it was re-introduced into Mexico (1991, CNMO 153) in imported strawberry seedlings, and has become a pest on cabbage crops in the State of Michoacán (Naranjo-García, unpublished data).

With regard to slugs, *Boetgerilla pallens* Simroth, 1912 (Table 3) is believed to be a pest in gardens and greenhouses in Europe (Welter-Schultes, 2012). Judging by their background record in other places of the world, *Deroceras reticulatum* (O.F. Müller, 1774), *Lehmannia valentiana* (Férussac, 1821), *Limacus flavus* (Linnaeus, 1758), *L. maximus* Linnaeus, 1758, *Rumina decollata* (Linnaeus, 1758) are potential pests on crops and gardens. *Deroceras reticulatum* is a very destructive slug that feeds on various cultivated plants (particularly at the seedling stage) such as cauliflower, cabbage, potato (Pilsbry, 1948; Castillejo, 1998). Hausdorf (2002) believes that *Deroceras invadens* Reise, Hutchinson, Schunack and Schlitt, 2011 is a serious pest.

Some authors consider *Deroceras laeve* (O.F. Müller, 1774) to as introduced in Mexico. However, there are fossil shells of what some believe to be this species of slug in Canada, the USA, and Mexico (El Cedral, San Luis Potosí; Olivera-Carrasco, 2007). If that is the case, the species has then been in North America since the Pleistocene. In Mexico, its two morphs are present, phallic (=euphallic) and aphallic. The species is well-suited with diverse life history traits that ensure it leaving descendants: it has a short life cycle, presents the two morphs, auto-fertilize, and, in rare occasions, present outcrossing. It is also tolerant of diverse ecological regimens and, under appropriate conditions, can reproduce all year long (Gómez, 2001; Jordaens et al., 2006). *Deroceras laeve* has been observed that become a pest in green houses (Wiktor, 2000).

The snail *Rumina decollata* in the area of Santiago, Nuevo León has been associated with crops of squash, onion, and cucumber (Correa-Sandoval, 1993).

Terrestrial species are *Sarasinula plebeia*, *Cornu aspersum*, *Paralaoma servilis* (Shuttleworth, 1852), *Arion circumscriptus*, *Deroceras laeve*, *Deroceras reticulatum*, *Lehmannia valentiana*, *Limacus flavus*, *Limax maximus*, *Rumina decollata*, *Oxychilus draparnaudi* (Beck, 1837) and *Zonitoides arboreus* (Say, 1816).

CONCLUSIONS

There are 56 species of mollusks introduced in Mexico. These records are confirmed by live material deposited in collections and from the literature. This number may increase as searches intensify. Until now, such information is contained in works consisting mostly of lists that do not indicate the status of the species treated and whether they are exotic (non-native) or invasive (established and naturalized). Species intentionally brought for aquaculture may contribute to the introduction of associated, potentially invasive species. Examples of this potential are mollusks with a byssus (mussels) and with live epifauna on the upper surface of an oyster.

Between 1980 and 2009, fewer than five authors have recorded living exotic species on the Mexican Pacific coast. Existing legislation should be applied rigorously or improved (Ortiz-Monasterio, 2014). Administration and management of ports and customs must protect the national territory and conserve biodiversity. Introduction of species can harm life cycles of other taxa, with direct damage to human health and the national economy.

Some of the mollusks here mentioned may succumb under the effects of climate change, but others may survive and colonize areas where they currently cannot survive due to the constraints imposed by the climate. Hence, it is important to know the status of each species, and to monitor their presence and effects over habitats and native wildlife at national level. Molecular studies will further add to the knowledge of the systematics and population structure of these alien species.

Mollusks are among the most biodiverse groups of invertebrates, and the creation of a Mexican monitoring network devoted to exotic species and their effects would help to protect native endemic species and could examine with scientific basis the effects of introduced organisms on human health and environment.

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A new species of *Lucinoma* from 240–500 m on the continental shelf break off Newfoundland (Bivalvia: Lucinidae)

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ABSTRACT

A new species of the lucinid bivalve genus *Lucinoma* is described from shells dredged at depths of 240–500 m from the edge of the continental shelf off southern Newfoundland. It differs from the other northern species, *Lucinoma filosa*, in shape, ligament, and characters of the anterior adductor muscle scar. It also differs from the poorly known *Lucinoma atlantis* from the outer shelf off Maryland that is longer than high and has both anterior and posterior sulci, and from *L. blakeana* from deep water off North Carolina, a smaller species with a truncate posterior margin. Other *Lucinoma* species are recorded further south in the northern Gulf of Mexico, particularly from hydrocarbon seeps, although the taxonomy is confused for those taxa.

INTRODUCTION

The chemosymbiotic Lucinidae is now recognized as one of the most speciose of marine bivalve families (Huber, 2015; WoRMS) and further new species and genera continue to be described (Glover and Taylor, 2016). *Lucinoma*, with at least 30 living species, is the best known and widespread of the deeper-water lucinid genera. The genus has a latitudinal range from 70° N to 55° S and from the intertidal zone to deeper than 2500 m (summary figure in Taylor and Glover, 2010, fig 5.9). The majority of *Lucinoma* species are found from >200 m to mid-bathyal depths and are often abundant at hydrocarbon seeps, mud volcanoes and oxygen minimum zones (Cary et al., 1989; Okutani and Hashimoto, 1997; Callender and Powell, 1997, 2000; Salas and Woodside, 2002; Olu-Le Roy et al., 2004; Holmes et al., 2005; Cosel, 2006; Cosel and Bouchet, 2008; Oliver and Holmes, 2006; Duperron et al., 2007; Oliver et al., 2012; Zamorano and Hendrickx, 2012). Around 40% of *Lucinoma* species have been described within the last 15 years suggesting that diversity has not yet been fully sampled. Nonetheless, it should be noted that some *Lucinoma* species reported from Japan (Okutani and Hashimoto, 1997), *L. adamsiana* Habe, 1958 and *L. japonica* Habe, 1958, are now classified in other genera and subfamilies (Glover and Taylor, 2016).

The phylogenetic placement of *Lucinoma* has been problematic. An initially surprising result from molecular analyses of Lucinidae was that *Lucinoma* species grouped within a major clade (subfamily Codakiinae) of otherwise largely shallow water species of *Ctena* and *Codakia* (Taylor et al., 2011; 2014; 2016). Previously, using shell characters, Dall (1901) had classified *Lucinoma* as a subgenus of *Phacoides*, a placement also followed by Britton (1970). By contrast, Chavan (1938; 1969) considered the genus to be related to *Myrtea* and placed it in the Myrteinae (also Abbott, 1974), while Bretsky (1976) classified it as a subgenus of *Miltha*. At species level *Lucinoma* are difficult to discriminate, but useful shell characters are: overall shape, form of commarginal sculpture, presence of posterior and anterior sulci, thickness of hinge line and size of cardinal teeth, presence/absence of anterior lateral teeth, and in particular, characters of the anterior adductor muscle scar, notably the length, width and angle of ventral detachment from the pallial line.

On the western Atlantic continental margin three species of *Lucinoma* have been described: *Lucinoma filosa* (Stimpson, 1851), *L. blakeana* (Bush, 1893), and *L. atlantis* (McLean, 1936). Unfortunately, only dead shells are available for study and no *Lucinoma* species from the Western Atlantic have been included in molecular analyses. Recently, we located in the collections of the Muséum national d'Histoire naturelle, Paris, several samples of a *Lucinoma* species collected in 1985 from dredging on the edge of the continental shelf off southern Newfoundland. These shells had been labelled as *Lucinoma filosa*, but differed from that species and also from the two other *Lucinoma* species described from the northwestern Atlantic. The samples were obtained during a survey of fish stocks (ERHAPS 851) in the territorial waters of Saint-Pierre and Miquelon, a small archipelago of French territory (*Collectivité d'Outre-mer de Saint-Pierre-et-Miquelon*) off the southern coast of Newfoundland. A narrow strip (10.5 nautical miles wide) of territorial waters (Exclusive Economic Zone) extends southwards across the continental shelf. Cosel (1986)

published a semi-popular account of the ERHAPS 851 cruise and a list of the mollusks recovered. In this paper we describe this new species of *Lucinoma* and compare it with congeners from the region.

MATERIALS AND METHODS

The length of anterior adductor muscle scars in relation to shell height and length were measured on shells using calipers, while measurements from *L. filosa* were mainly taken from scaled images of shell interiors from specimens in ANSP, USNM, and MCZ (latter images courtesy of G. Giribet and A. Baldinger). Similar measures were made from images of the holotypes of *L. blakeana* and *L. atlantis*. Outline drawings of shell interiors were made from digital images using Photoshop.

Institutional acronyms used: ANSP, Academy of Natural Sciences Philadelphia at Drexel University, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, The Natural History Museum, London, U.K.; USNM, United States Museum of Natural History, Washington, USA. Other abbreviations: aas, anterior adductor muscle scar; fms, fathoms; H, shell height; L, shell length; LV, left valve; pv, paired valves; RV, right valve; v, single left or right valve.

SYSTEMATICS

Bivalvia

Family Lucinidae Fleming, 1828

Subfamily Codakinae Iredale, 1937

Genus *Lucinoma* Dall, 1901

Type Species: *Lucina filosa* Stimpson, 1851 Original designation

Description: Medium to large shells. Subcircular to anteriorly tapering. Posterior sulcus with marginal sinus present in some species, anterior sulcus rarely present. Sculpture of narrow, regularly spaced, commarginal lamellae with finer lamellae between, radial sculpture absent. Lunule lanceolate, slightly sunken. Ligament long, external, protruding or in groove. Hinge with two cardinal teeth in each valve, larger teeth usually bifid, small to obscure anterior lateral teeth. Anterior adductor muscle scar usually long and detached from pallial line for about $\frac{3}{4}$ of length. Inner shell margin smooth.

Lucinoma thula new species

(Figures 1–13, 14–15)

Description: L to 70 mm, H to 63 mm, slightly longer than high ($H/L=0.94\pm0.04$, SD, $n=28$). Robust, subcircular, shallow posterior sulcus, posterior margin truncate

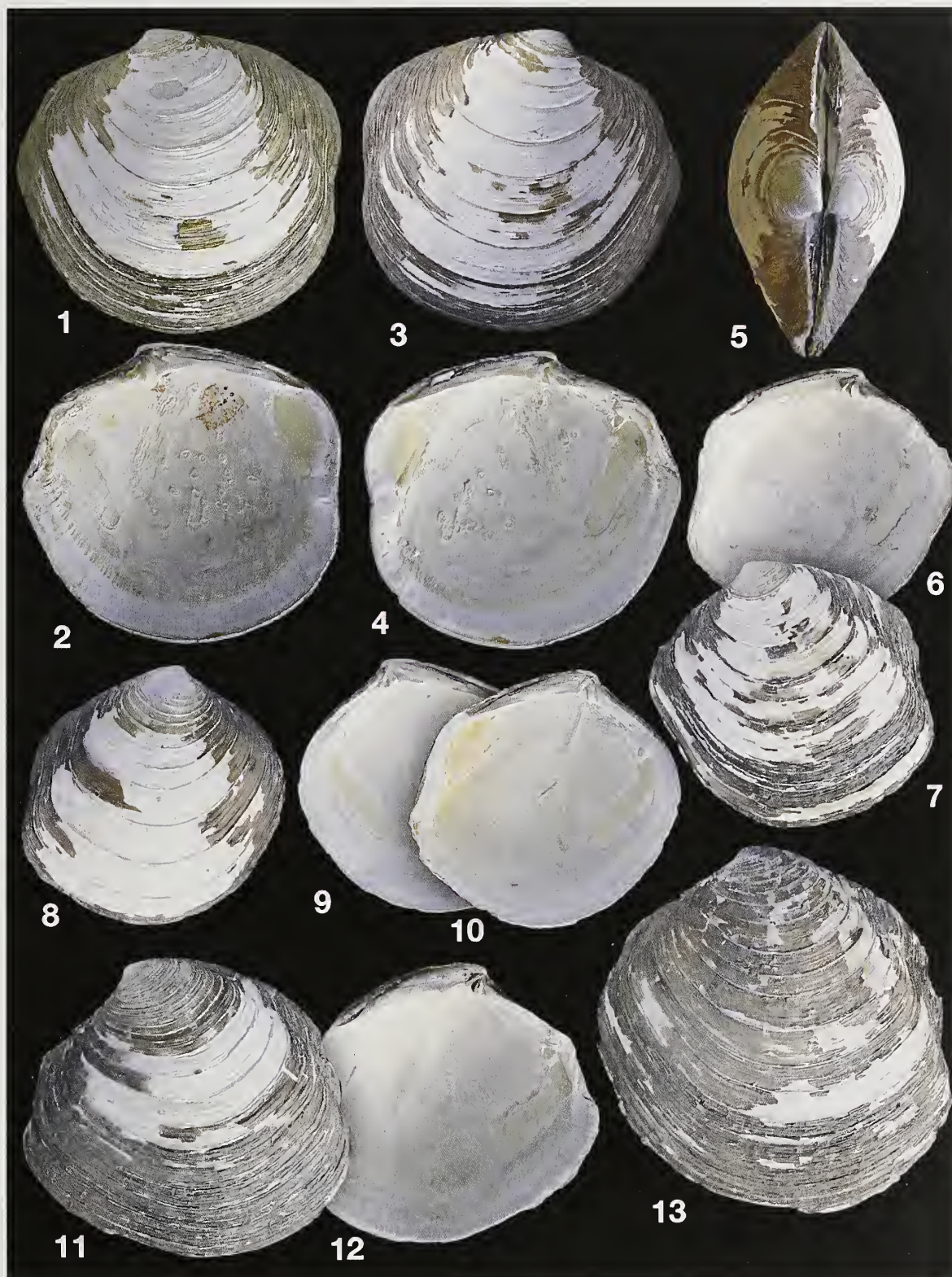
with shallow sinus, anterior margin slightly projecting, ventral margin broadly rounded. Umbones broad, low, prosogyrate. Periostracum: thick, dark olive-brown. Sculpture: widely spaced, low, sharp, commarginal lamellae with 5–7 finer commarginal “cords” in interspaces. Major lamellae are more closely spaced ventrally in larger shells. Lunule: long, lanceolate. Ligament: external, long, set on nymph. Hinge: RV with two cardinal teeth, anterior thin, posterior larger, slightly bifid, lateral teeth absent; LV with two cardinal teeth, anterior larger, slightly bifid. Anterior adductor muscle scar long, ventrally detached from pallial line at an angle of about 20° ; posterior adductor scar ovoid, anterior pedal retractor muscle scar separate and dorsal to anterior adductor scar. Pallial line entire, shell within line with subcircular scars of mantle attachment, pallial blood vessel trace visible, inner shell margin smooth.

Type Material: All type material from ERHAPS 851 cruise N.O. CRYOS. **Holotype:** One whole shell, Station L219, 345–512 m, $45^\circ01' N$, $54^\circ57' W$, 09 March 1985, L=61.3 mm, H=58.1 mm, tumidity single valve=15.2 mm, MNHN IM-2000-33102; **Paratypes:** MNHN IM-2000-33103, station L181, 310–308 m, $46^\circ32' N$, $57^\circ31' W$, 01 March 1985, 6 RV 9 LV (L=69.8, 57.2, 50.8, 54.8, 47.0, 45.8, 44.5, 40.3, 33.5 mm); MNHN IM-2000-33104, station L184, 243–244 m, $46^\circ21' N$, $57^\circ21' W$, 01 March 1985, 1 LV (L=55.6 mm); MNHN IM-2000-33105, station L185, 314–320 m, $46^\circ18' N$, $57^\circ22' W$, 01 March 1985, 1RV, 1LV, (L=53.5, 53.3 mm); MNHN IM-2000-33106, station L186, 282–278 m, $46^\circ12' N$, $57^\circ17' W$, 01 March 1985, 2 RV, 3LV (L=65, 55.2, 52.6, 51.5, 49.7 mm); MNHN IM-2000-33107, station L187, 323–322 m, $46^\circ05' N$, $57^\circ12' W$, 01 March 1985, 9 LV, 5 RV (L=56.3, 55.6, 52.8, 48.3, 47.7, 46.1, 44.6, 42.2, 42.1, 40.1, 37.9 mm); MNHN IM-2000-33108, station L189, 332–320 m, $46^\circ60' N$, $57^\circ04' W$, 02 March 1985, 2 pv (L=53.4, 36.6 mm); NHMUK 20170141, station L187, 323–322 m, $46^\circ05' N$, $57^\circ12' W$, 01 March 1985, two single valves (L=46.9, 44.3 mm).

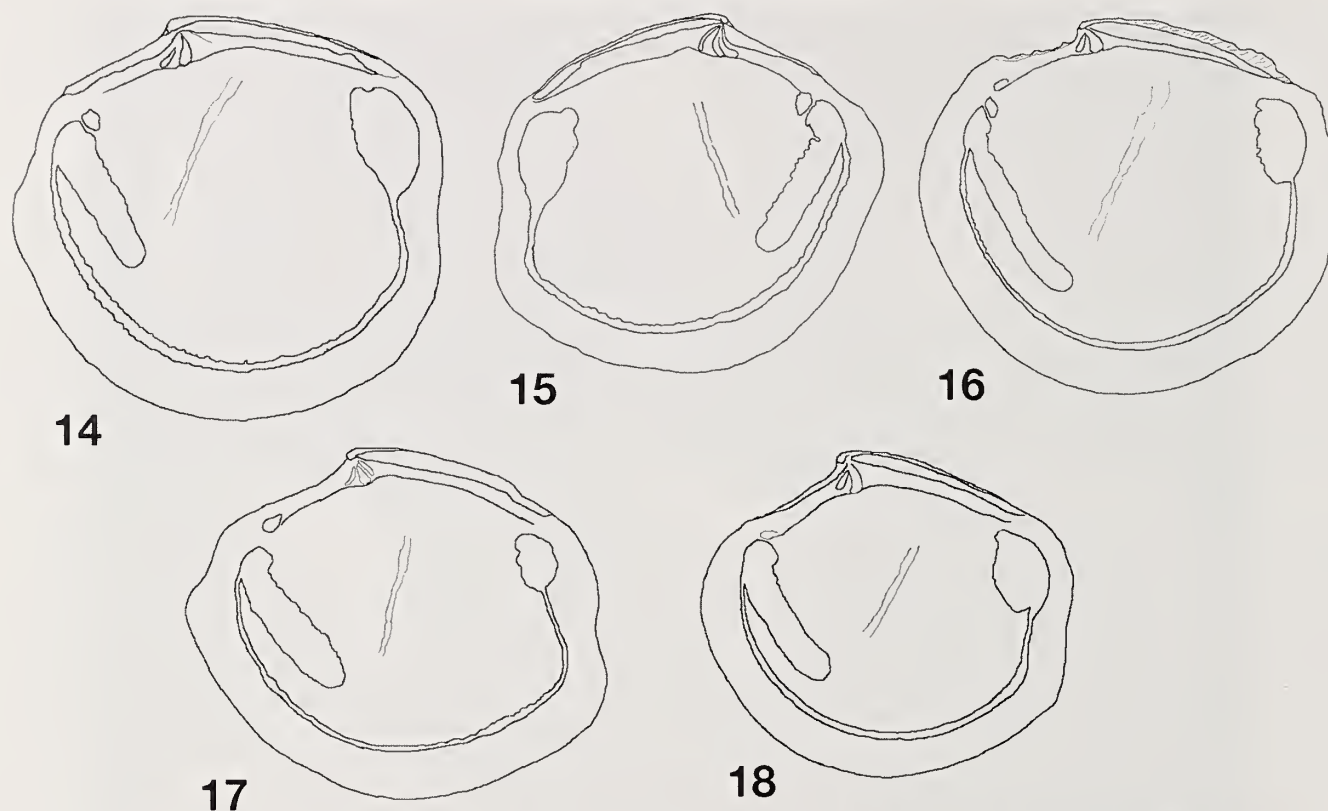
Habitat: Recorded from depths of 240–512 m near the edge of the continental shelf off southern Newfoundland. Rudo von Cosel (personal communication) reported that the sediment was fine to coarse sand and the accompanying fauna comprised “...regular sea urchins, lots of ophiurids, a few shrimps and large actinias, and among the mollusks mostly Buccinidae of different genera and species (17 in total).” See Cosel (1986) for a list of other mollusks recovered from the ERHAPS cruise but without details of individual stations.

Etymology: Derived from Latin *thule* for furthest north, in reference to the northerly location of the species.

Comparison with Other Species: The three *Lucinoma* species previously described from the northwestern Atlantic are illustrated in Figures 19–31 and their principal features documented below. The type localities of the northwestern Atlantic species are plotted in Figure 33.



Figures 1–13. *Lucinoma thula* new species, all specimens from ERHAPS 851 cruise. **1–5.** Holotype (MNHN IM-2000-33102), station L219, L=61.3 mm. **1–2.** Exterior and interior of left valve. **3–4.** Exterior and interior of right valve. **5.** Dorsal view. **6–7.** Paratype (NHMUK 20170141), station L187, interior and exterior of left valve, L=56.1 mm. **8–10.** Paratype (MNHN IM-2000-33103), station L181, exterior of right valve and interior of right and left valves, L=38.3 mm. **11–12.** Paratype (MNHN IM-2000-33106), station L186, exterior and interior of left valve, L=50.9 mm. **13.** Paratype (MNHN IM-2000-33106), station L 186, exterior of left valve, L=64.1 mm.



Figures 14–18. Internal drawings of valves. 14–15. *Lucinoma thula* new species. 14. Holotype 15. Paratype (NHMUK 20170141). 16. *L. filosa* (ANSP 102172). 17. *L. atlantis*, holotype. 18. *L. blakeana*, holotype.

***Lucinoma filosa* (Stimpson 1851)**

(Figures 16, 19–24, 34–35)

Brief Description: Shell length to 60 mm, subcircular, slightly longer than high ($H/L=0.88\pm0.02$ SD, $n = 12$), sculpture of regular, sharp commarginal lamellae. Slight posterior and anterior sulci. Lunule long, slightly sunken, Anterior dorsal margin elevated. Ligament in a groove with a deep escutcheon. Two cardinal teeth and vestigial anterior lateral tooth in each valve. Anterior adductor muscle scar very long and narrow, detached from pallial line for 4/5 of length (details below Figure 32). Periostracum relatively thin, pale tan, or buff.

Type Material: Not located (see Britton 1970, Bretsky 1976). The type locality (Stimpson, 1851:17) is cited as "...in 6 f sand near Pt Shirley (W.S.), Phillips Beach, alive after a storm (Holder)". Point Shirley is now in the town of Winthrop, a suburb of Boston, Massachusetts.

Distribution: *Lucinoma filosa* is distributed from Canada to Florida Keys and maybe into the Gulf of Mexico. It is well represented in collections from northern areas with recorded depths of 20–80 m but occurs in deeper water (to 400 m) further south off Florida Keys (Britton, 1970) (NHMUK20140794, see Figure 34–35). It was also recorded as common on the continental shelf in the Middle Atlantic Bight area, in less than 200 m,

between Cape Cod and Cape Hatteras (Wigley and Theroux, 1981: 95, fig. 76).

***Lucinoma atlantis* (McLean, 1936)**

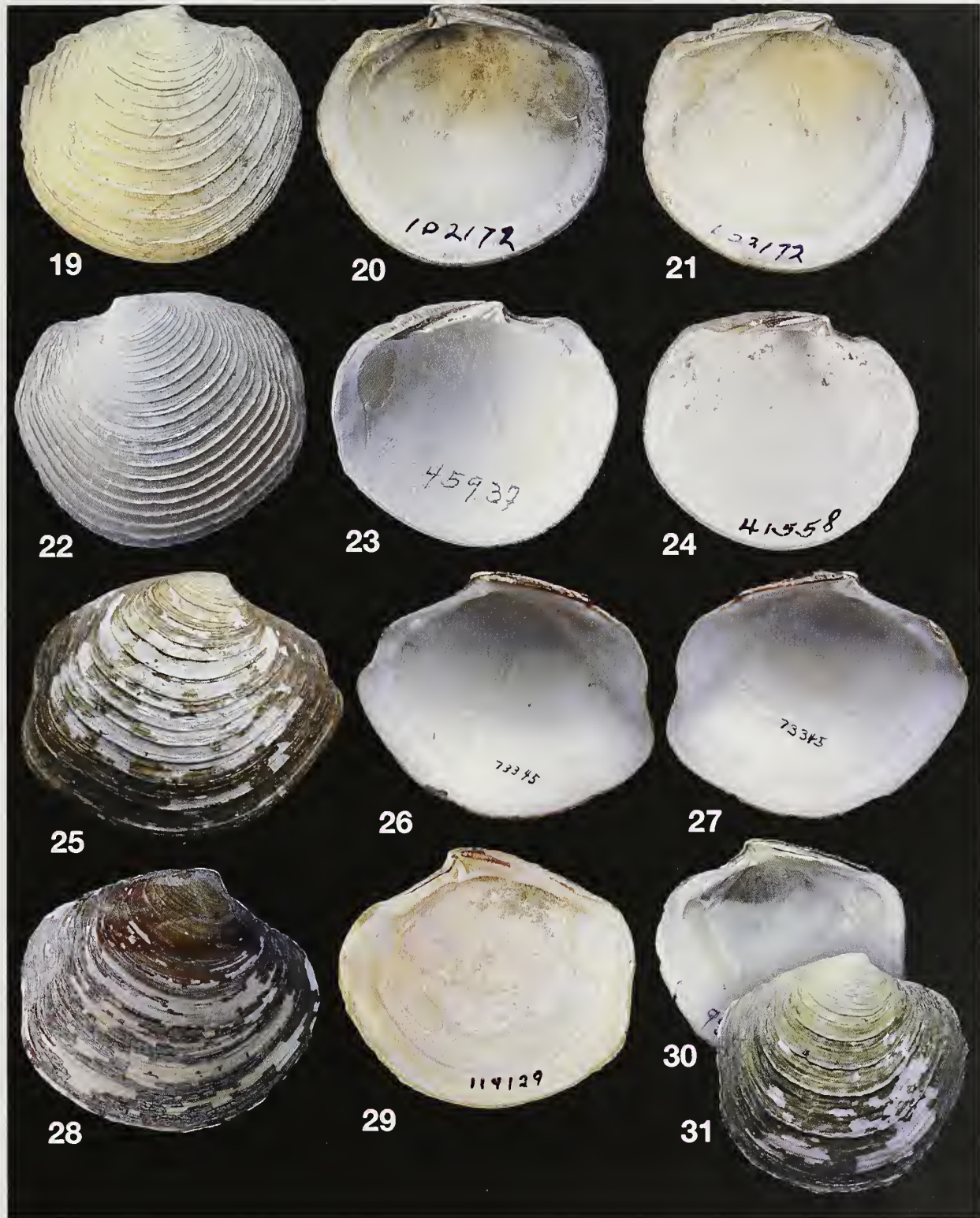
(Figures 17, 25–27)

Brief description: Holotype is longer than high, $H/L=0.81$, with widely spaced thin commarginal lamellae. Prominent anterior sulcus and posterior sulcus with marginal sinus. Larger of the two cardinal teeth bifid, distinct anterior lateral teeth in both valves. Anterior adductor muscle scar long, detached from pallial line for 3/4 of length. Periostracum thick and olive brown.

Type Material: Holotype, MCZ 73345, PV L=58.3 mm, H=47.3 mm

Type Locality: Off Maryland, 216–549 m, 38°10' N, 73°51' W (note coordinates on holotype label are incorrect) at edge of continental shelf.

Distribution: Known only from the holotype and we have seen no other comparable material. Bivalves identified as this species are widely reported from sites of hydrocarbon seeps off Louisiana in the northern Gulf of Mexico (Figures 39–46) (Turner, 1985: fig 2H; MacDonald et al., 1990; Callender et al., 1990; Callender and Powell, 1997) but specimens we have examined from



Figures 19–31. *Lucinoma filosa*, *L. atlantis* and *L. blakeana*. **19–21.** *Lucinoma filosa*, off Martha's Vineyard (ANSP 102172), L=39.4 mm. **22–23.** *L. filosa* (USNM 45937) exterior and interior of left valve, off Martha's Vineyard, 144 m, USFC stn 941, L=47 mm. **24.** *L. filosa* (MCZ 41558), interior of left valve, off New Jersey, 40° 01' N, 70° 30' W, 225 m, L=30.3 mm. **25–27.** *Lucinoma atlantis*, holotype (MCZ 73345) exterior of right valve and interior of right and left valves, off Maryland, 216–549 m, 38° 10' N, 75° 51' W, L=58.3 mm. **28–29.** *Lucinoma blakeana*, holotype (MCZ 119129), exterior and interior of right valve, off Cape Fear, North Carolina, 464 fms (850 m), Blake station 326, 33° 42' 15" N, 76° 00' 50" W, L=30 mm. **30–31.** *L. blakeana* (USNM 95694), exterior and interior of left and right valves, ALBATROSS Station 2677, 874 m, off Cape Fear, 32° 39' N, 76° 50' W, L = 41.6 mm.

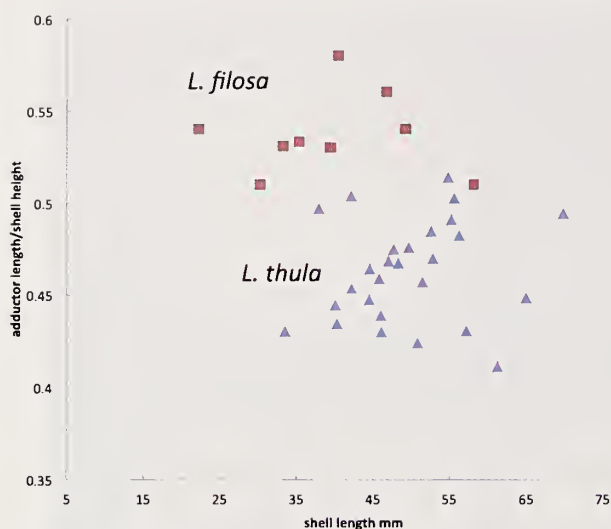


Figure 32. Comparison between *Lucinoma thula* and *L. filosa* in the relative length of the anterior adductor muscle scar (length of aas/shell height) plotted against shell length.

this region differ from the holotype of *L. atlantis* (despite the opinion of Turner, 1985) in lacking the anterior sulcus and thick, dark periostracum and likely represent a separate species.

***Lucinoma blakeana* (Bush, 1893)**

(Figures 18, 28–31, 36–38)

Type Material: Holotype MCZ 119129, single RV L=30.1 mm, H=26.9 mm, H/L=0.86.

Type Locality: Off Cape Fear, North Carolina, 850 m, BLAKE Expedition, 1880, station 326, 33°42' 15" N, 76°00'50' W.

Brief Description: Small species L to 30 mm longer than high, H/L=0.86, with a distinctive quadrate posterior margin and shallow posterior sulcus. Sculpture of widely spaced, thin, commarginal lamellae. Lunule long and lanceolate. Small anterior lateral teeth present in both valves and two cardinal teeth, larger bifid. Anterior adductor muscle scar long, ventrally detached from pallial line for ¾ of length. Periostracum of holotype is now tan brown but it was originally described (Bush, 1893) as thin and light yellow.

Distribution: Other specimens, also from off Cape Fear are USNM 92670, ALBATROSS station 2628, 966 m, and USNM 95694, ALBATROSS station 2677, 874 m, and similar shells are recorded from off Havana (Figures 36–38), USNM 64435, BLAKE station 43, on label as 24°08' N, 82°51' W, 449 fms (821 m); but the BLAKE station list in USNM records 339 fms (620 m) and 83°51' W for station 43. The few confirmed records available suggest that this is a much deeper water species than *L. filosa* and *L. thula*.

Remarks: A further *Lucinoma* species is represented by some shells from the northern Gulf of Mexico collected from Viosca Knoll lease block 826 (29°09' N, 88°01' W, depth ca. 450 m, off Alabama) and sent to Ruth Turner for identification (MCZ). These are illustrated in Figures 47–50. This is a large (L=81 mm, H=80 mm), rounded, inflated species, without significant sulci and with low commarginal lamellae that are much more closely spaced than the other *Lucinoma* from the northwestern Atlantic. The cardinal teeth are large with a small anterior lateral tooth in the left valve and the anterior adductor muscle scar is medium-length and broad. This species differs from the putative *L. atlantis* of the Gulf of Mexico and other western Atlantic *Lucinoma* species in shape, lack of sulci and the closely spaced lamellae. The taxonomy of all the *Lucinoma* species recovered from hydrocarbon seeps in the Gulf of Mexico remains problematic.

One of the main features that differentiates the new species, *Lucinoma thula*, from *L. filosa* is the length and position of the anterior adductor muscle scar; this is long and narrow in *L. filosa*, lying approximately parallel with the pallial line (Figure 16) and ventrally detached for 4/5 of length at an angle of about 12°. By comparison, in *L. thula* the adductor scar is shorter, broader, and diverges from the pallial line at an angle of about 20°. The relative lengths of the anterior adductor scar (as length/shell height) were compared: mean 0.46 ± 0.3 SD, $n=27$ for *L. thula* and 0.53 ± 0.2 SD, $n=11$ for *L. filosa* (Figure 32). These were significantly different (T test, $p > 0.05$). *Lucinoma filosa* has more closely spaced commarginal lamellae and is subcircular in outline but *L. thula* is posteriorly truncate. In most shells of *L. filosa* the postero-dorsal shell margin extends above the ligament (Figures 19–24), but not in *L. thula*. The periostracum is thicker and dark in *L. thula* compared to the pale and relatively thin periostracum of *L. filosa*.

The holotype of *Lucinoma atlantis* differs from *L. thula* in its markedly longer than high shell outline, distinct anterior and posterior sulcus (Figures 25–27), and visible anterior lateral teeth in both valves. *Lucinoma blakeana* is a smaller species (Figures 28–29) that differs in shape from *L. thula* and *L. filosa* with a quadrate posterior margin, only a slight posterior sulcus and a tan brown or yellowish periostracum compared with the darker olive brown of *L. thula* and *L. atlantis*.

DISCUSSION

It is probable that *Lucinoma thula* has been confounded with *L. filosa* in faunal surveys of the outer continental shelf and upper slope of the northwestern Atlantic but we have seen no other specimens in MCZ, ANSP, or USNM collections. From a macrobenthic survey of the northeastern USA continental shelf and slope, Theroux and Wigley (1998) recorded *L. filosa*, *L. blakeana* and *Lucinoma* sp. but gave no images or details.

Ideally, the taxonomic discrimination of *Lucinoma* species should be corroborated with molecular data. To



Figure 33. Map showing type localities of the *Lucinoma* species described from the eastern Atlantic seaboard of North America, and locations in the Gulf of Mexico of shells illustrated in Figures 34–52. Map from Google Earth Image 2017.

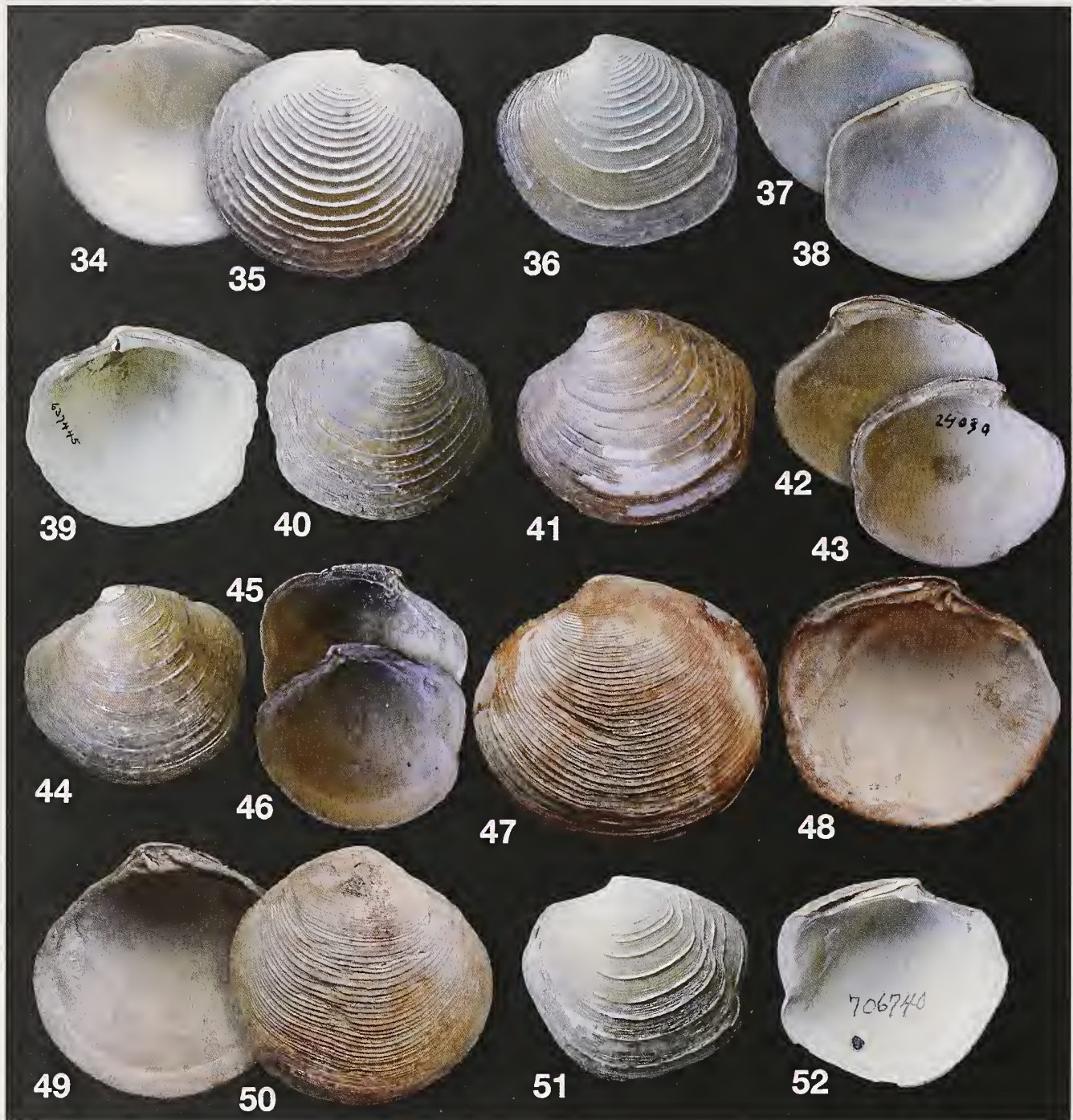
date only six species of *Lucinoma* have been included in molecular analyses; these originated from widely separated locations and depths but with none from the northwestern Atlantic. The species group in a well-supported clade with short branches and form a sister group to *Codakia* species (Taylor et al., 2016). Inclusion of the type species, *Lucinoma filosa*, and the other species from the western Atlantic is highly desirable. Nevertheless, the new species *L. thula* clearly differs morphologically from *L. filosa* and we are confident of its distinct identity. The northeastern Pacific species *Lucinoma annulata* (Reeve, 1850) has similar shape, sculpture, and musculature to *L. filosa* and may be a sister taxon. This species likewise occurs in shallow subtidal habitats at the northern end of its range in Alaska and in deeper water (665 m) at more southerly locations off Mexico (Coan et al., 2000). Described from a methane seep area in the eastern Pacific Ocean off Concepcion, Chile, *Lucinoma anemiophila* (Holmes, Oliver, and Sellanes, 2005) has a general similarity to *L. thula* but with more prominent anterior lateral teeth.

Recent surveys have revealed the presence of numerous sites of seafloor methane leakage along the northern US Atlantic margin (Skarke et al., 2014) and cold seep communities reported at depths as

shallow as 400–430 m in the Baltimore Canyon (<http://oceanexplorer.noaa.gov/explorations/12midatlantic/logs/aug26/aug26.html>) and others off Nantucket at 1100–1400 m (Quattrini et al., 2016). It is quite possible that the original specimens of *L. atlantis* and *L. blakeana* dredged from the edge of the continental shelf off Maryland and North Carolina (Figure 33) respectively might have been associated with cold seeps. Certainly, the latter species was recovered in the vicinity of extensive methane venting from the Blake Ridge gas hydrate province (Brothers et al., 2013). Similar sites of methane leakage are likely at the edge of the continental shelf off southern Newfoundland but there have been no biological surveys published, and, although it is possible that *L. thula* samples were trawled from such a site, we have no direct evidence. Cosel (1986) listed the macrofauna from the ERHAPS 851 survey but gave no details of individual stations; of 45 bivalve species recorded two other possible chemosymbiotic bivalves are *Solemya borealis* Totten, 1834 and *Thyasira* sp. (not all species harbour symbionts) but it is uncertain whether or not they co-occurred with *L. thula*.

Further to the south in the Gulf of Mexico several *Lucinoma* species have been reported associated with hydrocarbon seeps including putative *L. atlantis* (MacDonald et al., 1990; Cordes et al., 2000). Incidentally, some *Lucinoma* sp. reported from the hydrocarbon seeps are now assigned to other genera namely *Jorgenia* and *Gracina* and classified in the Myrteinae rather than Codakinae (Taylor and Glover, 2009). In the southern Caribbean, Gracia et al. (2012) reported three *Lucinoma* species (unnamed) from cold seeps at around 500 m off Colombia and, at depths of 230–800 off Guadeloupe, Taylor and Glover (2016) recorded two unnamed species from dead shells in poor condition.

Globally there is a strong association of *Lucinoma* species with seeps, as well as mud volcanoes and oxygen minimum zones. *Lucinoma myriamiae* (Cosel, 2006) occurs at seep sites from 360–425 m off West Africa (Sibuet and Vangreishheim, 2009); *Lucinoma taiwanensis* was described from an area of known hydrothermal activity off north Taiwan 205–650 m (Cosel and Bouchet, 2008), *Lucinoma yoshidai* is reported at Japanese seeps between 100–1000 m (Okutani and Hashimoto, 1997) and *Lucinoma anemiophila* from 780 m at a methane seep off southwestern Chile (Holmes et al., 2005). From the eastern Mediterranean, *Lucinoma kazani* was described from 1700 m deep mud volcanoes (Salas and Woodside, 2002; Olu-Roy et al., 2004) and *L. asaphaeus* from mud volcanoes in the Strait of Cadiz (Oliver et al., 2012). Additionally two species of *Lucinoma* are known from sediments in oxygen minimum zones; *L. aequizonata* from 400–650 m off southern California (Cary et al., 1989; Zamorano and Hendrickx, 2012; Hendrickx et al., 2016) and *Lucinoma gagei* from southern Oman at 675–967 m (Oliver and Holmes, 2006). *Lucinoma aequizonata* (Dall, 1901) has a remarkable tolerance of anoxia being able to survive 262 days without oxygen (Arndt-Sullivan et al., 2008).



Figures 34–52. *Lucinoma* specimens from northern Gulf of Mexico. **34–35.** *Lucinoma filosa* (NHMUK20140794), interior and exterior of RV, SW of Marquesas Rock, Florida Keys, 24°20.62' N, 82°16.41' W, 185–195 m, L=35.5 mm. **36–38.** *Lucinoma blakeana* (USNM 64435), exterior of LV and interior of RV and LV, off Havana, BLAKE station 43, 24°08' N, 82°51' W, 821 m, L=22.3 mm. **39–40.** *Lucinoma "atlantis"* (USNM 637445), interior and exterior of RV, Gulf of Mexico, 27°50' N, 91°11' W, 375 m, L=38 mm. **41–43.** *Lucinoma "atlantis"* exterior of LV and interior of RV and LV, Garcia collection no 24039, off Louisiana, Bush Hill seep site in lease block Green Canyon 185, 27°46.904' N, 91°30.286' W, 546–555 m, L=48.6 mm. **44–46.** *Lucinoma atlantis* exterior of LV and interior of LV and RV, Garcia colln no 24039, Off Louisiana, Bush Hill seep site in lease block Green Canyon 185, 27°46.904' N, 91°30.286' W, 546–555 m, L=53.5 mm. **47–50.** *Lucinoma* sp. (MCZ), off Alabama, Viosca Knoll lease block 826, 29°09' N, 88°01' W, ca. 450 m (Figures 47–48, L=81 mm; 49–50, L=80 mm). **51–52.** *Lucinoma* sp. (USNM 706740), off Tortugas (no details), 347–512 m, L=46 mm.

The fossil history of *Lucinoma* also reveals an association with hydrocarbon seep habitats. Although *Lucinoma*-like lucinids first appeared in the early Cenozoic in shallow water Paleocene deposits (Taylor et al., 2011) maybe as a sister clade to *Saxolucina*, they have been associated with fossil deep-water hydrocarbon seeps since the Oligocene; for example, *L. hannibali* (Clark, 1925) (Kiel, 2010; Nesbitt et al., 2013) and in the Italian Miocene *Lucinoma perusina* (Sacco, 1901) (Moroni, 1966). Massive accumulations of *Lucinoma* shells are recorded at sites of fossil seeps in the Miocene and Pliocene of Japan with inferred palaeo-depths of 50–300 m (Majima et al., 2003, 2005).

Continuing discoveries of hydrocarbon seeps, gas hydrates, pockmarks, mud volcanoes (e.g., Cunha et al., 2013; Quattrini et al., 2015) shows that these habitats are abundant along the margins of continental shelves. The biological communities associated with many of these have yet to be investigated and the focus of the better known sites has concerned epifaunal or shallowly infaunal bivalves, *Bathymodiolus* and *Vesicomyidae* (Olu-LeRoy et al., 2007; Cordes et al., 2009) with deeper burrowing taxa such as *Lucinoma* less well sampled or studied. Improved sampling and accompanying molecular studies should clarify the confused taxonomy of the Gulf of Mexico and wider Caribbean *Lucinoma* species and their relationships to the more northerly species along the eastern USA continental margin. From the research activity at hydrocarbon seeps in the northern Gulf of Mexico relatively few *Lucinoma* samples have been archived in museum collections despite their apparent abundance, as evidenced for example by Callender and Powell (1997).

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Bayerotrochus belauensis, a new species of pleurotomariid from the Palau Islands, western Pacific (Gastropoda: Pleurotomariidae)

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ABSTRACT

A new pleurotomariid species, *Bayerotrochus belauensis* new species, collected from the Palau Islands, western Pacific, is described and illustrated. This new species is most similar in shell morphology to *B. teramachii* (Kuroda, 1955), from which it may be distinguished by its thinner, lighter shell with a taller, more stepped spire and lack of pronounced spiral sculpture along the shell base. Molecular data (COI) show *B. belauensis* new species to be more closely related to *B. boucheti* from New Caledonia and *B. delicatus* from Yap, than to *B. teramachii*. *Bayerotrochus boucheti* (Anseeuw and Poppe, 2001) differs in having a broader, more conical spire, a more depressed aperture, and a more darkly pigmented shell with spiral sculpture on the shell base. The recently described *B. delicatus* S.-P. Zhang, S.Q. Zhang, and Wei, 2016 is easily distinguished by its much smaller size and distinctive shell profile.

Additional Keywords: Slit shell, COI, phylogeny, ecology.

INTRODUCTION

Bayerotrochus Harasewych, 2002 is the most widely distributed of the Recent pleurotomariid genera. It includes 12 living species, two inhabiting bathyal depths of the temperate and tropical western Atlantic, and ten from similar depths along the margins of the Indian and western Pacific Oceans. Ongoing sampling of deep-sea biota using dredges and trawls, as well as manned and remotely operated research submersibles, in addition to analyses of relationships among samples using molecular techniques, continue to expand and refine our knowledge and understanding of the biodiversity and biogeography of the deep oceans and their faunas.

Two samples of living *Bayerotrochus* were first observed and collected off Palau at depths around 200 m by the Japanese research submersible HAKUYO in

October of 1996 (Okutani and Kurata, 1998). They were provisionally identified as *Perotrochus africanus teramachii* (Kuroda, 1955) based on shell morphology. During subsequent explorations at similar depths in Palau in 2001 using the research submersible DEEPWORKER 2000, Coral Reef Research Foundation (CRRF) was able to observe, photograph, and collect additional specimens of that species of *Bayerotrochus*. Shells and tissues of several of these samples were deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). Most recently, Zhang et al. (2016) described *Bayerotrochus delicatus* from Yap Seamount (8°51' N, 137°47' E), SE of Yap near Nguluu Atoll, collected at slightly greater depths (255–289 m). A phylogenetic analysis based on partial COI sequence data that was included in their description showed that *B. delicatus* was more closely related to one of the specimens from Palau (USNM 905395) than to *B. teramachii*.

These results prompted our re-examination of the Palau specimens, which were compared morphologically against all species of *Bayerotrochus* known from the Indian and Pacific Oceans. Results of these morphological comparisons as well as a phylogenetic analysis of COI sequences derived from three of the Palau specimens and additional *Bayerotrochus* sequences, both published and previously unpublished, indicate that the Palau samples differ from all other species of *Bayerotrochus*, and are here described as a new species.

MATERIALS AND METHODS

Radular Morphology: The radula was dissected from the alcohol-preserved holotype, cleaned in 10% NaOH overnight, rinsed in distilled water, cleaned in an ultrasonic cleaner, air dried, coated with gold, and photographed using a Leica StereoScan 440 Scanning Electron Microscope.

Molecular Procedures: Genomic DNA was extracted from alcohol-preserved tissue samples (c. 25 mg buccal muscle) using the DNeasy Tissue Kit (Qiagen) following

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the manufacturer's animal tissue protocol. A 658 bp portion of the cytochrome c oxidase I gene was amplified using the primers of Folmer et al. (1994). PCR amplifications used the Promega GoTaq hot start master mix (Promega M7132) according to manufacturer's instructions, but modified to reduce the reaction volume to 20 μ L. Cycling parameters: initial denaturation at 95°C for 3 minutes, followed by 45 cycles of denaturation at 94 °C for 30 seconds, annealing at 45°C for 45 seconds and extension at 72 °C for 2 minutes, with final extension at 72°C for 5 minutes. Resulting PCR products were visualized by agarose gel electrophoresis (1.5% garose) and purified with ExoSAP-IT (Affymetrix). Sequencing reactions were performed using 1 μ L of purified PCR product in a 10 μ L reaction containing 0.5 μ L primer, 1.75 μ L Big Dye buffer and 0.5 μ L Fig Dye (Life Technologies). Reactions were run for 30 cycles of 95°C for 30 seconds 50°C for 30 seconds and 60°C for 4 minutes then held at 12°C. Reactions were purified using Millipore Sephadex plates and sequenced on an ABI 3730XL automated DNA analyzer. Sequencher v. 4.7 (Gene Codes) was used to visualize, trim and assemble contigs from forward and reverse sequences. The sequences have been deposited in GenBank (NCBI). Accession numbers are provided in Table 1.

The COI sequences were aligned using MUSCLE within Geneious (v. 9.1.6; <http://www.geneious.com>, Kearse et al., 2012) and trimmed to the 658 bp region

flanked by the Folmer primers. The phylogenetic tree (Figure 28) was produced using the RAXML 7.2.8 (GTR Gamma nucleotide model) plugin in Geneious 9.1.6. Institutional acronyms are listed on Table 1.

SYSTEMATICS

Class Gastropoda Cuvier, 1795

Order Vetigastropoda Salvini-Plawen, 1980

Family Pleurotomariidae Swainson, 1840

Genus *Bayerotrochus* Harasewych, 2002

Type Species: *Perotrochus midas* Bayer, 1965, by original designation.

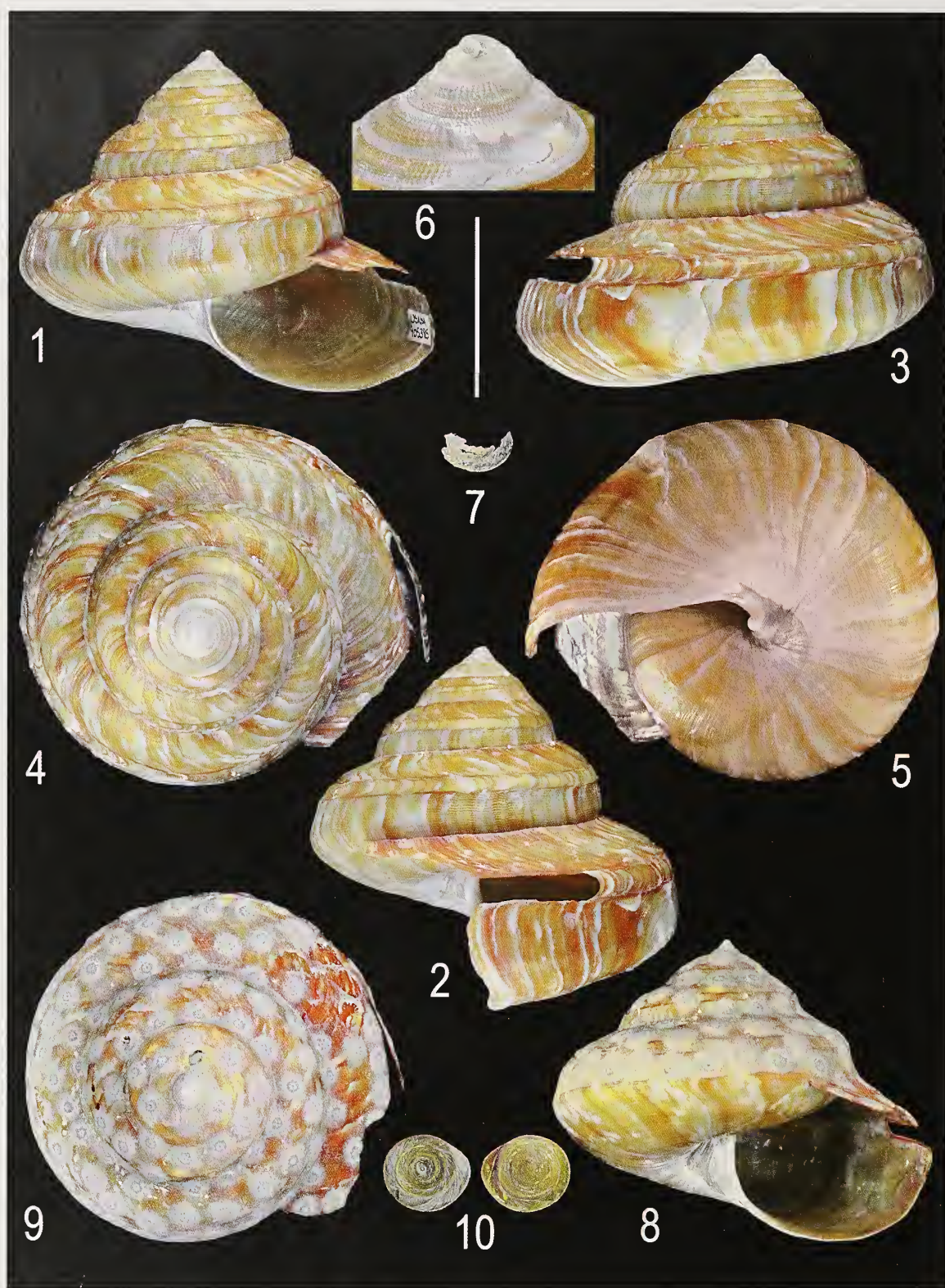
Description: Shell large, thin, turbiniform, lacking an umbilicus, with inflated, rounded whorls. Slit, broad, short (<90°), forming a selenizone slightly below mid whorl. Outer prismatic layer of shell thin, translucent, sculpture usually limited to spiral threads or weak cords and axial riblets that may produce weakly reticulate sculpture on early whorls. Aperture large, ovate. Operculum small relative to aperture.

Remarks: *Bayerotrochus* is easily distinguished from *Entemnotrochus*, which is characterized by having a large, conical shell with a narrow, long (>120°) slit and a deep

Table 1. Sources for the cytochrome c oxidase I sequence data used to produce the phylogenetic tree in Figure 28.

Taxon	Locality	Voucher	Genbank No.	Reference
<i>Calliostoma torrei</i>	Jacksonville, FL, USA	USNM 1069300	DQ 314293	Harasewych and Sedberry, 2006
<i>Lischkeia imperialis</i>	Guadeloupe	USNM875107	KY426958	This study
<i>Entemnotrochus rumphii</i>	Anami-O-Shima, Japan	USNM888698	L78911	Harasewych et al., 1997
<i>Entemnotrochus adansonianus</i>	Marathon, FL, USA	USNM 1089839	KY432515	This study
<i>Entemnotrochus adansonianus</i>	SW Navassa Is., Haiti	USNM 878151	KY432516	This study
<i>Entemnotrochus adansonianus</i>	Curaçao	USNM 1297226	KY432517	This study
<i>Perotrochus quoyanus</i>	Dominica	USNM 1410044	KY432518	This study
<i>Perotrochus amabilis</i>	Marathon, FL, USA	USNM1080832	KY432519	This study
<i>Perotrochus gotoi</i>	Amami-O-Shima, Japan	Not available	KY432520	This study
<i>Perotrochus caledonicus</i>	New Caledonia	MNHN-IM-2007-36301	KR087190	Anseeuw et al., 2015
<i>Perotrochus deforgesii</i>	Chesterfield Plateau	MNHN-IM-2007-32061	KR087208	Anseeuw et al., 2015
<i>Mikadotrochus beyrichi</i>	Boso Peninsula, Japan	Not available	AM049331	Williams and Ozawa, 2006
<i>Mikadotrochus beyrichi</i>	Boso Peninsula, Japan	Not available	EU530109	Williams et al., 2008
<i>Bayerotrochus midas</i>	Altamaha, Georgia, USA	USNM 1069299	KY432521	This study
<i>Bayerotrochus midas</i>	Great Inagua, Bahamas	USNM 1072411	KY432522	This study
<i>Bayerotrochus midas</i>	Roatan Is., Honduras	USNM 1155020	KY432523	This study
<i>Bayerotrochus teramachii</i>	Okinawa, Japan	Not available	AM049330	Williams and Ozawa, 2006
<i>Bayerotrochus teramachii</i>	Kagoshima, Japan	USNM 869646	KY432524	This study
<i>Bayerotrochus delicatus</i>	SE of Yap, Micronesia	MBM283051	KU759008	Zhang et al., 2016
<i>Bayerotrochus boucheti</i>	New Caledonia	MNHN-IM-2009-7484	KU693173	Anseeuw, 2016
<i>Bayerotrochus boucheti</i>	Chesterfield Plateau	MNHN-IM-2007-34676	KU693174	Anseeuw, 2016
<i>Bayerotrochus boucheti</i>	New Caledonia	MNHN, sta. DW2031	KY432525	This study
<i>Bayerotrochus belauensis</i> HT	N Turtle Cove, Palau	USNM 905395	KY432526	This study
<i>Bayerotrochus belauensis</i>	Mutremdiu 2, Palau	USNM 905393	KY432528	This study
<i>Bayerotrochus belauensis</i>	Mutremdiu 3, Palau	USNM 905397	KY432527	This study

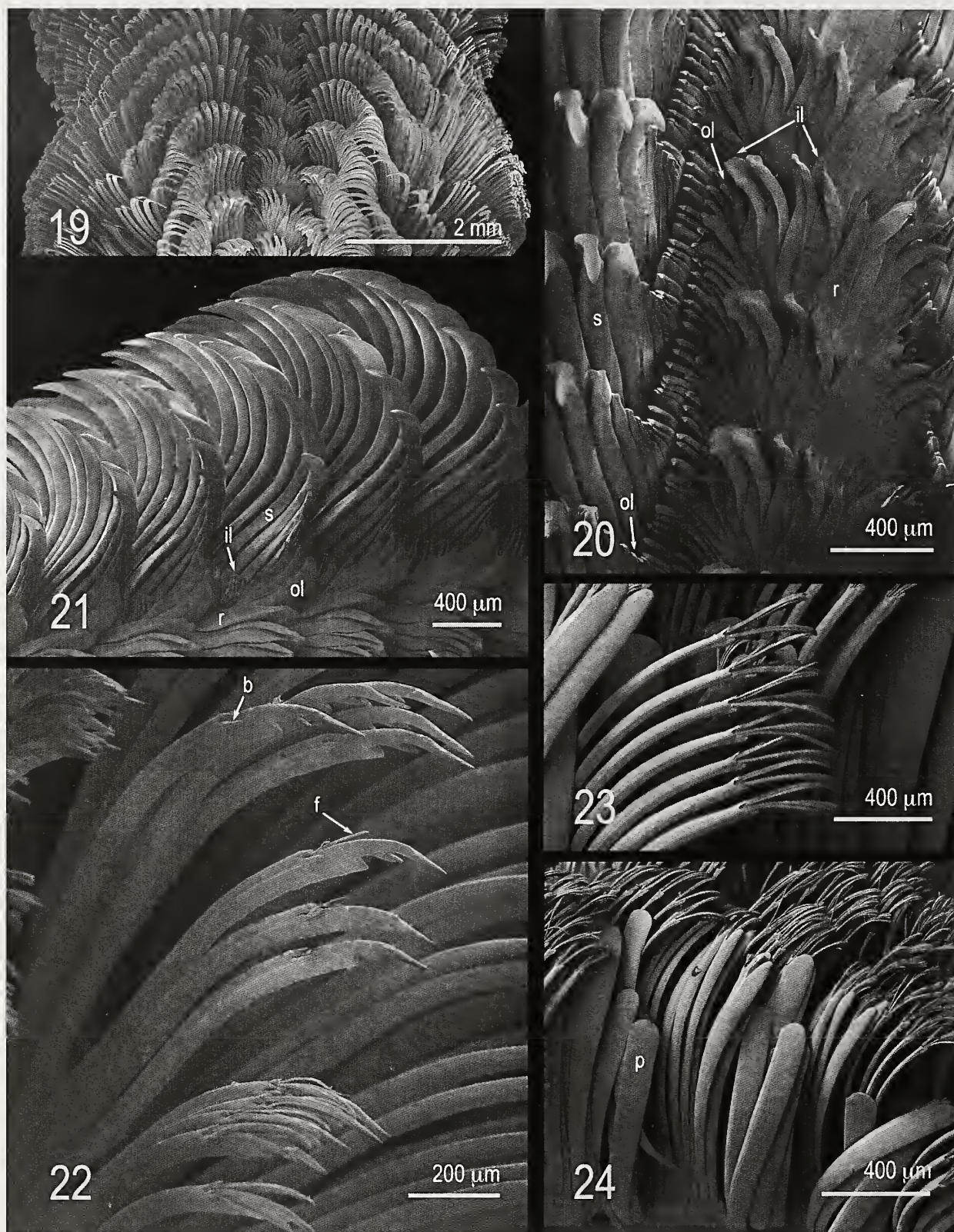
Institutional acronyms: MBM, Marine Biology Museum, Chinese Academy of Sciences, Qingdao; MNHN, Museum national d'Histoire naturelle, Paris; USNM, National Museum of Natural History, Smithsonian Institution, Washington



Figures 1–10. *Bayerotrochus belauensis* new species. **1.** Apertural, **2.** lateral, **3.** dorsal, **4.** apical, and **5.** basal views of holotype (USNM 905395). Palau Islands, North Turtle Cove, 219 m, 26 March 2001. **6.** Detail of early whorls. **7.** Outer surface of damaged operculum of holotype. **8.** Apertural and **9.** apical views of Paratype 1 (USNM 905397). Palau Islands, Mutreindin 3, in 236 m, March 24, 2001. **10.** Outer and inner surfaces of the operculum of Paratype 1. Scale bar = 5 cm for all shells and opercula, 1 cm for figure 6.



Figures 11–18. Apertural and basal views of: **11–12.** *Bayerotrochus teramachii*, S.W. of Makurazaki, Kagoshima, Japan trawled 350 m, **13–14.** *B. cf. teramachii*, off Panglao, Bohol, Philippines, by native fishermen using tangle nets set at 100 m., **15–16.** *B. westralis*, Rowley Shoals, N.W. Australia, Timor Sea, by shrimp trawler in 580 m. **17–18.** *B. boucheti*, S.E. New Caledonia, trawled in 550 m. Scale bar = 5 cm for all specimens. All specimens in Anseeuw Collection.



Figures 19–24. Radula of holotype of *Bayerotrochus belauensis*, new species. **19.** Extended radula. **20.** Rachidian, inner lateral and outer lateral teeth. Teeth to the left of the rachidian are further anterior than their homologues to the right. **21.** Sickle teeth. **22.** Transition from sickle teeth to filament-tipped teeth marked by onset of bristles. **23.** Detail of distal ends of filament-tipped teeth near the outer margin of the radula. **24.** Paddle-shaped teeth, showing transition from filament-tipped teeth. Abbreviations: **b**, bristle; **f**, filament; **il**, inner lateral teeth; **ol**, outer lateral teeth; **p**, paddle-shaped teeth; **r**, rachidian; **s**, sickle teeth.

umbilicus. It may be distinguished from *Perotrochus* and *Mikadotrochus* by its larger, thinner, more rounded shell. Sequence data from several genes (18S and COI) also readily distinguish among the genera of living Pleurotomariidae (e.g., Harasewych, 2002: 269; Zhang et al., 2016: 258).

***Bayerotrochus belauensis* new species**

(Figures 1–10, 19–27)

Perotrochus africanus teramachii: Okutani and Kurata, 1998: 11, figs. 2, 3. (not of Kuroda, 1955)

Description: Shell (Figures 1–6, 8, 9) large for genus (to 114.6 mm diameter), thin, turbiniform, with conical spire and rounded base, non-umbilicate, consisting of 8+ whorls. Spire coeloconoid (spire angle = 87°–99°), with shoulder increasingly pronounced after fifth whorl. Protoconch unknown. Selenizone narrow, situated at mid-whorl in early whorls, becoming broader, descending to just below the shoulder by fifth whorl. Axial sculpture of prosocyrtr riblets on early whorls (Figure 6) that form beads at intersections with spiral cords above and below selenizone. Ribs, cords, and beads become reduced above the selenizone by fourth teleoconch whorl. Spiral cords below selenizone remain more pronounced, with 14–16 weak cords persisting onto the last whorl between the selenizone and shell periphery. Selenizone with opisthocyrtr ribs on early whorls that transform to spiral cords by fourth whorl and subsequently decrease in prominence. Selenizone on last whorl with coarse, prosocyrtr growth striae. Slit broad (to 7.5 mm), short (75°–79° between limit of suture and rear of slit). Suture adpressed. Basal disc strongly and evenly convex, with sigmoidal growth striae more pronounced than weak spiral threads (Figure 5).

Aperture broadly elliptical (w/h = 1.3–1.5), deflected from coiling axis by ~81°–85°. Outer lip thin, smooth, portion below slit offset from portion above slit by 36°–51°. Columella spirally coiled, with sigmoidal flexure near the adapical margin. Aperture nacreous, columella porcellaneous. Base color of prismatic layer of shell exterior white, with broad, irregular axial bands of light-orange tan and narrower bands of darker reddish-orange. Shell may appear lustrous to varying degrees, depending on thickness / translucence of the prismatic layer. Operculum (Figure 10) amber-colored, multispiral, corneous, small (spanning 0.5 of minor axis of aperture).

Radula: Radula (Figures 19–24) of holotype (shell = 114.6 mm maximum diameter) 97.7 mm long, 6.7 mm wide, asymmetrical, left-skewed, bifid posteriorly, composed of 148 inverted V-shaped teeth rows. Following Hickman's (1984) terminology, each row consists of a single rachidian tooth, 4 inner lateral, 30 outer lateral, 13 sickle, ~58 filament-tipped, and 8–9 paddle-shaped teeth. Transitions between adjacent tooth types are gradual, and may span 2–6 teeth. Tooth morphologies

are similar to those of other species of *Bayerotrochus* and *Perotrochus*.

Type Locality: Palau Islands, Peleliu State, North Turtle Cove, 07°05.12 N, 134°15.61 E, 219 m.

Type Material: Holotype, USNM 905395 (shell and preserved animal) from the type locality, collected 26 March 2001 by Patrick L. Colin; Paratype 1, USNM 905397 (shell and preserved animal), Palau Islands, Koror State, Mutremdiu 3, Uchelbeluu Reef, 07° 16.27 N, 134°31.37 E, in 236 m, collected 24 March 2001 by Patrick L. Colin; Paratype 2 USNM 905396 (preserved animal only), shell in the Patrick Anseeuw Collection, Palau Islands, Koror State, Mutremdiu 3, Uchelbeluu Reef, 07°16.27 N, 134°31.37 E, in 232 m, collected 21 March 2001 by Patrick L. Colin; Paratype 3, USNM 905393 (preserved animal only), shell in the Etpison Museum, Palau Islands, Koror State, Mutremdiu 2, Uchelbeluu Reef, 07°16.41 N, 134°31.43 E, 212 m, collected 12 March 2001, by M.N. Dawson.

Etymology: *Belau*, the name of the Palau Islands in the Palauan language.

Ecology: In Palau this new slit shell was seen and collected on four out of over 60 submersible dives from both rock and sediment substrates at depths from 210–235 m (Figures 25–27). Submersible operations were conducted for many hours both above and below these depths, but no pleurotomariids were observed outside this depth range. Both of Okutani and Kurata's (1998) specimens were from 200 m, implying perhaps a limited depth range for this species along the outer reef slopes of the Palau Islands.

Downwelling light at these depths was relatively low, although there was still sufficient light to maneuver the submersible around large objects without additional lighting. The water is extremely clear. Temperatures at 200–250 m depth along Palau's outer reefs are generally about 10–13°C.

Overall the outer island slopes in Palau are steep, averaging about 30°–45°. The geomorphology of the outer slope has vertical escarpments, steep rocky slopes and more gentle sediment slopes. No slit shells were seen on any vertical to very steep slopes, although such profiles occurred in the species' depth range. Where seen, observations of slit shells were on both sediment and hard bottoms with slopes from about 25° to 45°.

The new slit shell was observed once apparently feeding on the sea pen *Anthoptilum grandiflorum* at 212 m depth during the day (Figure 25). The snail was on the downslope side of the sea pen with its foot extended and wrapped around the exposed base of the sea pen. Potentially it was digesting tissue around the central pen; the same sea pen has an area slightly above that shows damage, perhaps due to earlier feeding by the mollusk. These fleshy whip-like sea pens occurred only on sediment bottoms in clusters of individuals, their basal bulb buried in the gently sloping bottom.



Figures 25–27. *Bayerotrochus belauensis*, new species, *in situ* photographs. 25. Paratype 3, station Mutremdiu 2, in 212 m. 26. Paratype 2, station Mutremdiu 3, in 232 m. 27. Holotype, station North Turtle Cove, in 220 m.

This sea pen was only observed at depths between 190 and 240m, coinciding with the observed range of the snail.

Comparative Remarks: Morphological similarities among many of the Indo-Pacific species of *Bayerotrochus* have led to the reluctance of some researchers to distinguish populations from throughout the broad range of the genus as separate species (e.g., Abbott and Dance, 1982; Okutani and Goto, 1984; Okutani and Kurata, 1998; Williams and Ozawa, 2006). More recent studies, some based on larger sample sizes and supplemented with molecular data, have led to the recognition of ten Indo-Pacific species within *Bayerotrochus* (Bouchet, 2016).

Among its geographically proximal congeners, *Bayerotrochus belauensis* new species more closely resembles *B. teramachii*, *B. westralis*, and *B. boucheti* than the smaller species *B. poppei*, *B. philpoppei*, and *B. delicatus*, which can be readily distinguished on the basis of size, spire profile, and surface sculpture. This new species is conchologically most similar to the widespread *B. teramachii*, which ranges from Honshu, Japan through the East and South China Seas to the Sulu Sea (Anseeuw & Goto, 1996), and particularly to specimens attributed to this species from Panglao, Bohol, Philippines.

Japanese specimens of *B. teramachii* (Figures 11–12) are similar to *B. belauensis* new species in adult size, but have a less stepped shell profile, thicker and heavier shells that are less lustrous, have more pronounced spiral ribs on the base, and weaker axial growth lines on the apical whorls. Specimens from Panglao that have been provisionally identified as *B. cf. teramachii* (Figures 13–14) more closely resemble *B. belauensis* new species than Japanese *B. teramachii* in spire angle and profile, color and luster of the shell surface and aperture shape. Additional research will be required to more precisely determine the relationships of this population from Panglao.

Bayerotrochus westralis (Figures 15–16) resembles *B. belauensis* new species in adult size and in having a thin, light shell with a short slit and similar sculpture on its early whorls. However, *B. belauensis* new species differs in having a narrower, more stepped spire, a smoother, more lustrous surface and a broader selenizone. *Bayerotrochus boucheti* (Figures 17–18) is also comparable to *B. belauensis* new species in size, but differs in having a more heavily pigmented shell with a more conical, less stepped spire, a more depressed aperture shape, and in having more pronounced spiral sculpture on the basal disk.

Molecular Analysis: Partial sequences of the cytochrome c oxidase I gene spanning 658 bp were obtained from the holotype and two paratypes of *B. belauensis* new species, and a maximum likelihood tree (Figure 28) was produced that included the samples itemized in Table 1. This analysis resulted in a single, fully resolved tree that recovered the monophyly of *Bayerotrochus*, segregated the Atlantic from the Pacific clades, and differentiated the species *B. teramachii*, *B. delicatus*, *B. boucheti*, and

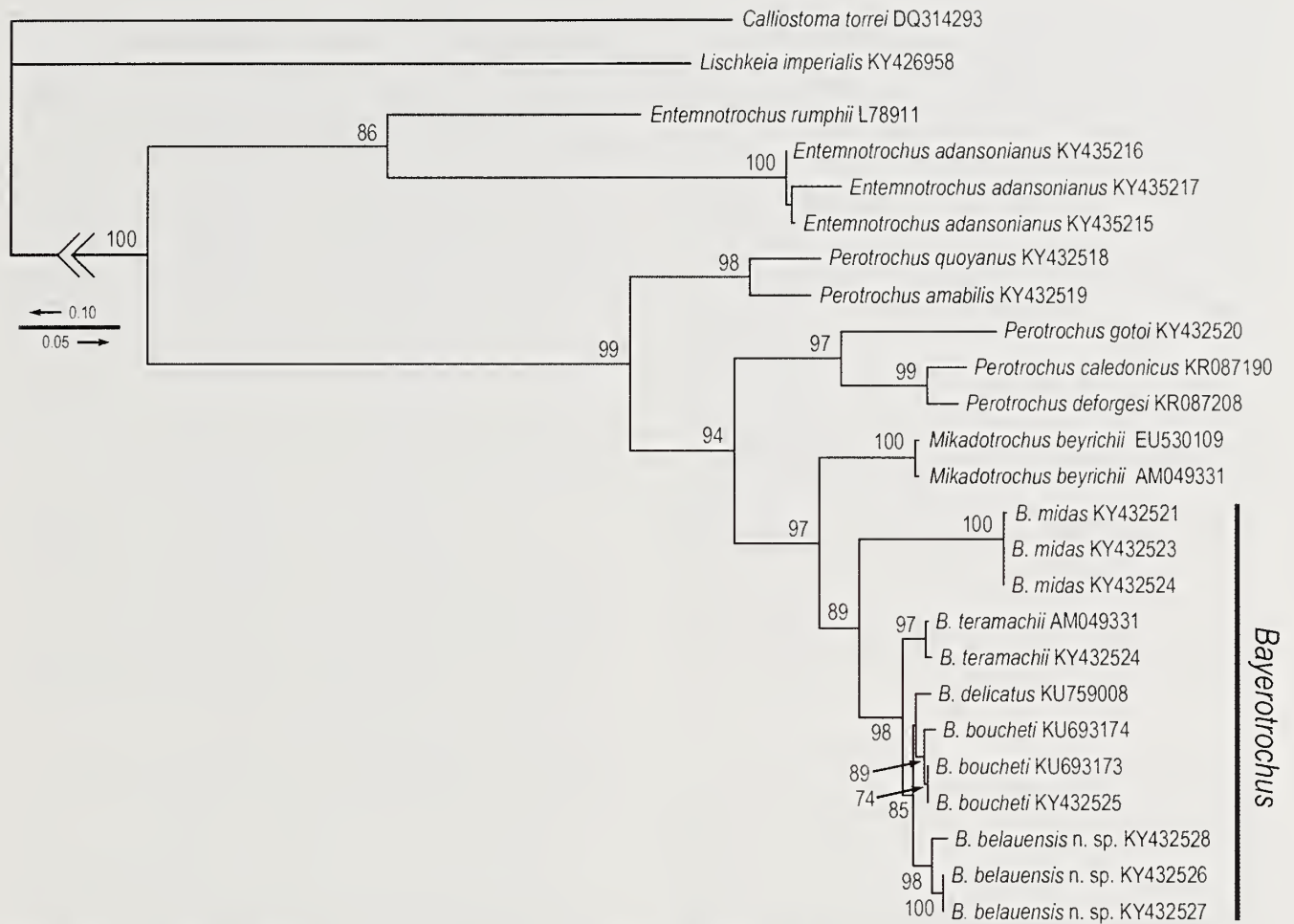


Figure 28. Maximum likelihood (RAxML) analysis of phylogenetic relationships among pleurotomariid taxa based on partial COI sequences. Numbers adjacent to nodes indicate bootstrap values ≥ 50 .

B. belauensis new species, all with high levels of support. These data indicate that *B. belauensis* new species is more closely related to *B. boucheti* and *B. delicatus* than to *B. teramachii*.

DISCUSSION

Based on morphological criteria, specimens of *Bayerotrochus* collected off Palau had been identified as being conspecific with the Japanese species, *B. teramachii* (Okutani and Kurata, 1998). Molecular data from a specimen from this population (USNM 905395, as *Bayerotrochus* sp.) was used in a more recent study describing a new species of *Bayerotrochus* from Yap (Zhang et al., 2016) and revealed that the Palau specimens were not closely related to *B. teramachii* and likely represented a new species. Sequence data from additional Palau specimens as well as from several other Indo-Pacific *Bayerotrochus* confirm that this population from Palau represents a distinct species that is more closely related to

B. boucheti and *B. delicatus* than any of these species are to Japanese *B. teramachii*.

Specimens from a population of *Bayerotrochus* from Panglao (Figures 13–14) that were previously identified as *B. cf. teramachii*, are morphologically very similar to, and possibly conspecific with the Palau species described here. Additional sampling and molecular studies will be needed to determine the relationships of this population and perhaps revise the range of *B. teramachii*.

Transects along the tropical western Atlantic conducted using submersibles revealed that pleurotomariids species and genera are not sympatric, but inhabit well demarcated, non-overlapping bathymetric zones, each corresponding to a specific bottom topology and habitat (Harasewych, 2002: fig. 12). *Entemnotrochus* species are the shallowest and those of *Bayerotrochus* the deepest dwelling taxa along any transect. Similar data is not yet available for Indo-Pacific species. Although the specimens of *Bayerotrochus belauensis* new species occur at shallower depths than their western Atlantic and most Indo-Pacific congeners (Harasewych, 2002: fig. 12A), their

habitat, including inclination of the slope and the substrate, appear similar.

Three of the four individuals collected had most of the shell covered with an unidentified zoanthid, *Epizoanthus* sp. (Figures 8, 9, 26, 27). The specimen observed feeding on the sea pen lacked zoanthids. Anseeuw and Goto (1996) also report the growth of zoanthids on shells of some species, but attribute no benefit to this relationship, describing it as parasitic growth. Zoanthids are known to possess some of the most potent toxins found in marine organisms and it is likely the covering of toxic zoanthids may provide some protection from predation. Large fishes may be deterred from ingesting whole or crushing the shell by the living sheath of zoanthids. Despite having had an overgrowth of zoanthids (Figure 27), the holotype of *B. belauensis* new species (Figures 1–6) shows evidence of numerous repaired breaks indicating multiple episodes of unsuccessful predation by shell-breaking predators, possibly large crustaceans. Larger sample sizes would help to clarify potential correlations between zoanthid overgrowth and incidence of unsuccessful predation. *Bayerotrochus belauensis* was the largest gastropod found during more than 60 submersible dives off Palau.

ACKNOWLEDGMENTS

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A redescription of *Rissoina mayori* Dall, 1927, a junior subjective synonym of *Opalia pumilio* (Mörch, 1875) (Gastropoda: Epitoniidae)

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ABSTRACT

An examination of the type material of *Rissoina mayori* Dall, 1927, confirmed that Ponder (1983) was correct in allocating the species to the family Epitoniidae. It is here redescribed and a lectotype is designated. Because of the similarity in shell characters and the overlap in geographic range, we consider *R. mayori* and *Opalia pumilio* (Mörch, 1875) to be synonyms.

Additional Keywords: New synonym, western Atlantic, Rissoidae

INTRODUCTION

In 2015, Marien Faber, who has been researching the Rissoininae, contacted us regarding *Rissoina mayori* Dall, 1927. He was looking for our opinion on whether this species was referable to the Rissoininae as proposed by Dall, or to the Epitoniidae, as proposed by Ponder (1983: 90).

Neither Dall nor Ponder provided figures of the species, nor, apparently, has it been critically discussed or figured elsewhere in the literature. To resolve this question, we contacted Yolanda Villacampa and Dr. Ellen Strong at the Smithsonian Institution's National Museum of Natural History (USNM), requesting photographs of material of this species in the USNM type collection. They provided the scanning electron microscope (SEM) photographs reproduced here.

After reviewing the SEM photographs and the type material, it became apparent that Ponder was correct in his placement. This species indeed seems to belong to the Epitoniidae. Because this species has, to date, been overlooked in reviews of western Atlantic epitoniids, we herein redescribe and illustrate this species.

SYSTEMATICS

Family Epitoniidae S. S. Berry, 1910

Genus *Opalia* H. and A. Adams, 1853

Type Species: *Scalaria australis* Lamarck, 1822, type of *Clathrus* Gray, 1842.

Opalia pumilio (Mörch, 1875)

Scala (*Opalia*) *subvaricosa* var. *pumilio* Mörch, 1875: 268
Rissoina mayori Dall, 1927 **new synonym** (Figures 1, 2, 3)

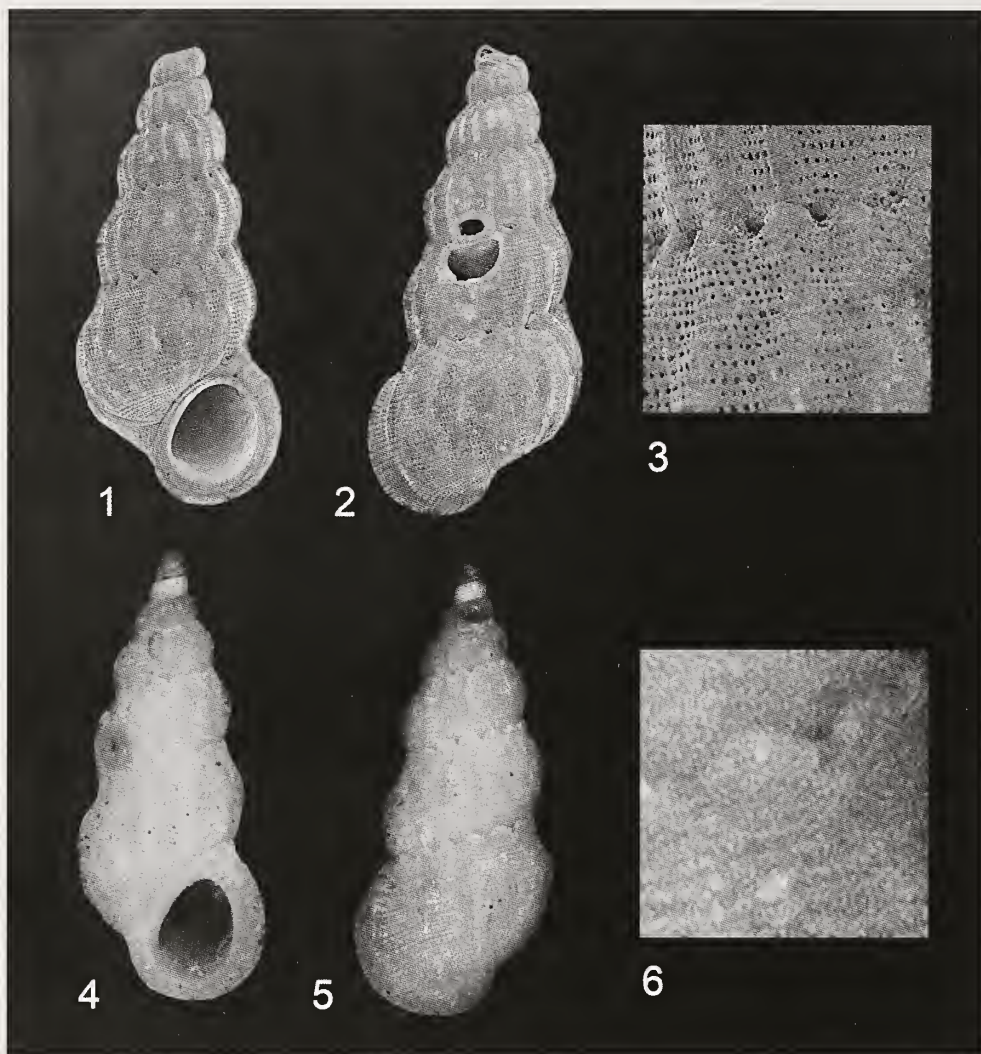
Description of *Rissoina mayori*: Lectotype (Figures 1, 2, 3) 4.2 mm in length (apex missing), 1.8 mm in diameter, imperforate and sculptured. Color white. Five+ convex teleoconch whorls; suture strongly crenulated, aperture obliquely ovate, outer lip thickened. Costae strong on the early whorls, but weaker on the rounded base of the body whorl; 15 costae on the body whorl, including one that is thickened and varix-like. Intervals with minute spiral striae, separated by rows of punctae. Operculum unknown.

Type Material: Lectotype of *Rissoina mayori* Dall, 1927, USNM 108371, here designated.

Type Locality: Off Georgia, 30°44' N, 79°26' W, 440 fms [= 805 m], ALBATROSS station 2415 (Dall 1927: 1, 105).

Remarks: Dall (1927: 105) referred to *Rissoina mayori* one specimen from Station 2415 which is due east of Cumberland Island, Georgia, as well as material collected off Miami in 58 fathoms. There is no indication on the label that Dall designated the specimen collected from Station 2415 to be the holotype. The material collected off Miami was not located in the USNM collection. (Y. Villacampa, personal comment, 15 April 2015). Therefore, we consider these specimens to be syntypes and are designating USNM 108371 to be the lectotype.

Because *Rissoina mayori* has crenulated sutures and a pitted intritacalx, we are referring this species to the genus *Opalia*. This is consistent with Bouchet and Warén (1986: 54), who referred to the genera *Gregorioiscula* Cossmann, 1912, and *Punctiscala* de



Figures 1-6. *Opalia* species. 1-3. *Rissoina mayori*, lectotype USNM 108371, 105 miles off Georgia, 30°44' N, 79°26' W, 805 m, ALBATROSS station 2415. 4-6. *Scala (Dentiscala) hellenica nodosocarinata* Dall, 1889 [= *Opalia pumilio* (Mörch, 1875)], holotype USNM 82955, 5 miles off Cape Florida, Florida, 15 m, 3.9 mm.

Boury, 1890, species with non-crenulated sutures and a strong basal disk over which the costae do not extend and who referred to the genus *Opalia* species with crenulated sutures that may or may not have a basal disk.

Based on the material at hand, *Rissoina mayori* appears to be indistinguishable from *Opalia pumilio* (Mörch, 1875). The shell characters cited in Clench and Turner (1950: 238) for *O. pumilio* are certainly applicable to Dall's species. While the holotype of *Scala nodosocarinata* Dall, 1889 (a synonym of *O. pumilio* [Clench and Turner, 1950: 237]) (Figures 4, 5, 6) appears to differ from *R. mayori* in having finer pitting and raised ridges on the teleoconch whorls, it is not clear that these differences are taxonomically significant, given the fact that *O. pumilio* is "...an exceedingly variable species" (Clench and Turner, 1950: 238). Furthermore, the known range of *R.*

mayori, from Cumberland Is., Georgia, south to Miami, Florida, is well within the range of *O. pumilio*. In fact, the type locality for *Scala (Dentiscala) nodosocarinata* Dall, 1889, is 5 miles off Cape Florida, Florida, a locality that could be considered to be Miami, Florida.

ACKNOWLEDGMENTS

We want to thank Marien Faber for bringing this problematic species to our attention. We also want to thank Dr. Ellen Strong and Ms. Yolanda Villacampa at the USNM for providing us with the photographs of the type material for *R. mayori* and *S. hellenica nodosocarinata* and for allowing us to examine the type material of these two species. We wish to thank Patrick Zinn at Texas A&M University for creating the plate.

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Erratum

The recent article by Miyajima et al. (2017) was published with an earlier, incorrect version of Figure 55. The correct version of that illustration is included here. The new version includes the corrected species name *Adulomya* sp. 1 in the figure legend, replacing the originally submitted name *Adulomya* sp. A.

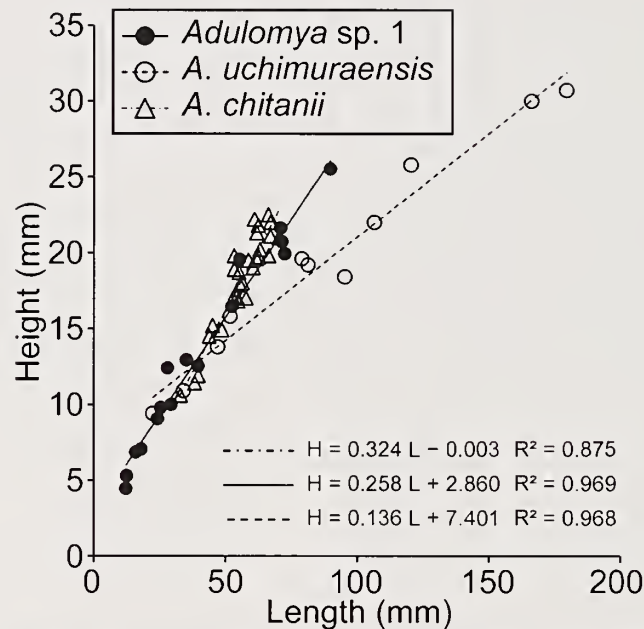


Figure 55. Relationships between shell length and height with growth of *Adulomya* sp. 1 from Loc. 2, *A. uchimuraensis* Kuroda, and *A. chitanii* Kanehara. Measurements of *A. uchimuraensis* and *A. chitanii* are from Kanno et al. (1998) and Amano and Kiel (2011), respectively.

LITERATURE CITED

Miyajima, Y., T. Nobuhara, and H. Koike. 2017. Taxonomic reexamination of three vesicomyid species (Bivalvia) from the middle Miocene Bessho Formation in Nagano Prefecture, Central Japan, with notes on vesicomyid diversity. *The Nautilus* 131: 51–66.

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